A review of rainforest pollination and plant-pollinator interactions with particular reference to Australian subtropical rainforests

Geoff Williams[1,2] and Paul Adam[1]
[1]School of Biological Sciences, University of New South Wales, Sydney, New South Wales 2052
[2]Department of Entomology, The Australian Museum, 6–8 College Street, Sydney, New South Wales 2000

ABSTRACT

Pollination is an essential process in the life cycle of most flowering plants and thus maintenance of the process is necessary for the long-term maintenance of rainforest ecosystems and their associated biota. As rainforest stands become fragmented will disruption of plant/pollinator relationships result in further decline of ecosystem diversity?

The spatial and temporal distribution of resources in rainforest is reviewed, and the patterns of resource availability suggest that generalist rather than specialist plant-pollinator relationships will be more common, and this may confer resilience to the ecosystem in the face of environmental perturbation. However, individual plant species, in particular those with highly co-adapted plant-pollinator relationships, and species in which breeding success is strongly population density-dependent, may be at risk if rainforest ecosystems are fragmented.

Information on pollination in rainforests is reviewed, with especial attention being given to subtropical rainforests such as occur in New South Wales. The evidence supports the prediction of the importance of generalist insect dominated pollination systems, at least for trees and large shrubs, but attention is drawn to a number of cases where specialist interactions have been demonstrated. It is suggested that thrips may be the pollinators of a number of species.

There are few data on the pollination ecology of Australian subtropical rainforests. In view of the importance of pollination for long-term conservation of rainforest, a number of important avenues for future research are suggested.

INTRODUCTION

Rainforests are widely recognized as the great storehouses of terrestrial biodiversity and the continuing loss of rainforest is a matter of international concern. Australian rainforests are now very limited in extent (Adam 1992) but contain a large proportion of national biodiversity.

During the 1980s substantial advances were made towards the conservation of Australian rainforests. These advances were made ahead of knowledge of the ecology of rainforest and the scientific basis for the long term management of what are often fragmented stands is still to be developed. An important topic of concern is regeneration. General accounts of the regeneration process are given by Floyd (1990), Summerbell (1991) and Adam (1992), but details of particular aspects of the process are poorly known. Individual plant species may be vulnerable to disturbances that result in a reduction in breeding success (House 1993) and local extinction. Over large contiguous areas of rainforest there may be kaleidoscopic changes in species distribution at the local scale over time, so that overall diversity is maintained but as the habitat becomes fragmented then patches may diverge markedly and both plant species and their associated fauna may become lost. The combinations of patterns of disturbances and availability of progagules are so complex that detailed prediction of the course of regeneration in individual patches is at present impossible (Hubbell 1979; Primack and Hall 1992; Williams 1993). Reserves established for the conservation of some particular combination of biota may only fulfil their desired function for a limited period. To assess the viability of reserves, and to manage them to meet particular conservation objectives, will require much greater understanding of regeneration processes and plant breeding systems.

Subtropical rainforest is a major component of the New South Wales rainforest (Adam 1987), but the most diverse stands, those in lowland sites, have been massively fragmented (Floyd 1990). Are these remnants, if sympathetically managed, potentially viable in the long term or will they gradually fade away? The viability will, to a large extent, depend on whether or not regeneration processes, including pollination, are maintained. There is little information on pollination in subtropical rainforest, either in Australia or overseas; we hope this review will serve as stimulus for further studies.

In this review we first address the need for pollination and for pollination vectors. The nature of pollinator-plant interactions may be influenced by the spatial and temporal patterns of availability of floral resources so that we next consider these issues. Over evolutionary time scales fluctuations in the extent of rainforest may have influenced the development and stability of plant-pollinator relationships.

In considering these topics most of the available data refer to non-Australian forests, although Australian examples are quoted whenever possible.

Specialist species

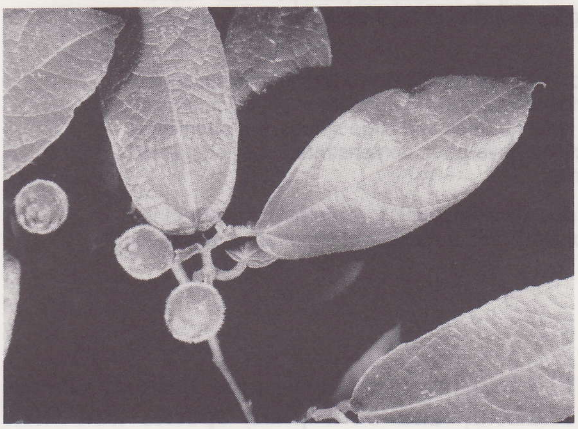

Figure 1. Ficus coronata (Moraceae). Fig species are pollinated by minute wasps in the family Agaonidae although few Australian *Ficus* species have been investigated. Fig–agaonid relationships are generally considered to be host-specific but some exceptions have been recorded in which more than one agaonid has been recorded from a single species of fig. (All photos by G. Williams).

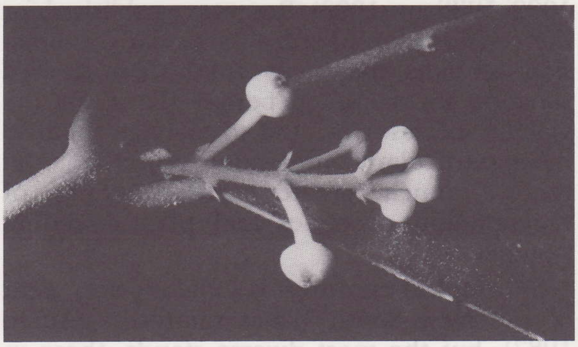

Figure 2. Specialized thrip-pollinated flowers of *Wilkiea huegeliana* (Monimiaceae). The three apical flowers are males, larger basal flowers are female. The fused cap-like perianth separates from the receptacle, following pollination and subsequent fertilization, to expose numerous developing carpels. Although, occurring on the flowers of many rainforest plants, thrips (Thysanoptera) have been recorded as pollinators of subtropical rainforest trees, shrubs and vines that possess partly fused (e.g., *Rapanea*) or complex (e.g., *Maclura*) flowers that generally deny access to other pollinators.

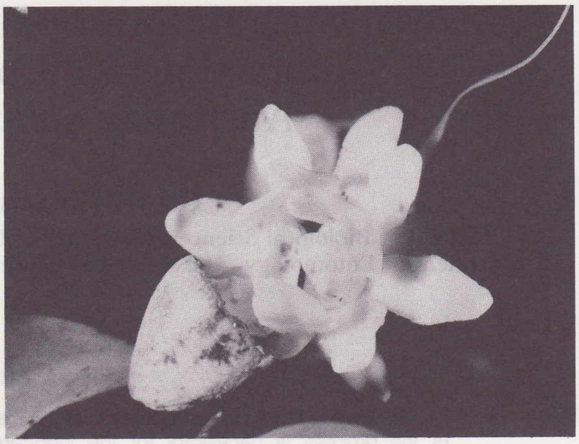

Figure 3. "Operculum" being shed on anthesis of *Eupomatia laurina* (Eupomatiaceae). The Eupomatiaceae retain floral structures thought to characterize the hypothetical primitive angiosperm condition and are pollinated by weevils in the genus *Elleschodes*. The weevils oviposit in the flowers which later act as a food substrate for developing weevil larvae.

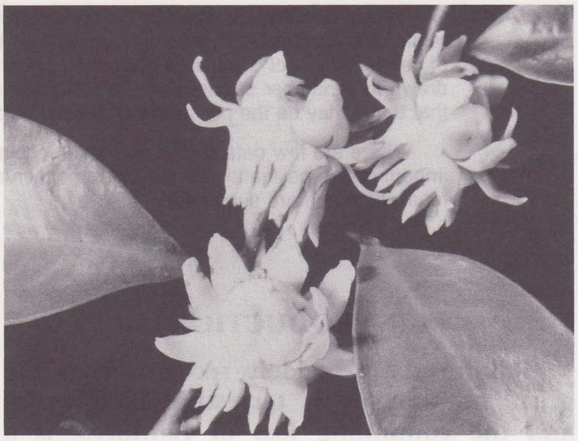

Figure 4. Eupomatia laurina. Eupomatia does not possess a perianth. "Flowers" are formed by basally united stamens and large fleshy staminodes, collectively called the synandrium. The synandria absciss approximately 14–30 hours after anthesis carrying developing *Elleschodes* larvae away from the gynoecium.

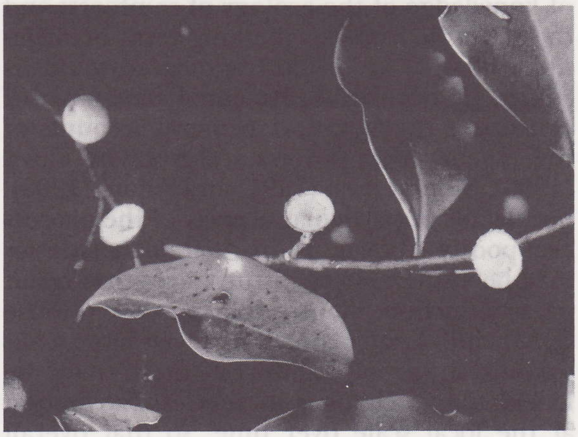

Figure 5. Developing *E. laurina* gynoecia immediately following abscission of synandria.

At least for canopy trees the hypothesis can be advanced that the spatial and temporal (both short and long term) availability of floral resources of a single species will favour generalist rather than specialist plant pollinator relationships, and this is supported by much of the available data. Given that cross pollination is desirable, and in some cases is obligatory, the movement of vectors between plants is considered. Few of the studies of this topic are from Australia.

In studies of floral biology and pollination ecology there has been a tradition of seeking to recognize syndromes of morphological and physiological characteristics of flowers which are associated with particular pollination vectors. We discuss various syndromes which have been recognized in the literature and attempt where possible to provide examples from subtropical rainforest. Examples of subtropical rainforest plants with specialist (Figs 1–5) and generalist (Figs 6–8) relationships with pollinators are illustrated.

General reviews of pollination biology were provided by Proctor and Yeo (1975), Faegri and van de Pijl (1979), Raven, Evert and Curtis (1982), Kevan and Baker (1983) and Bertin (1989), while Dafni (1992) and Kearns and Inouye (1993) provide reviews of techniques for the study of pollination ecology. Biotic pollination mechanisms in the Australian flora were reviewed by Armstrong (1979). Australian pollination study references are cited in Kearns and Inouye (1993) and a pollination biology database has been compiled by Inouye (1993). The following treatment draws heavily on these sources.

POLLINATION AND BREEDING SYSTEMS

The Importance of Pollination

Pollination is an essential process in sexual reproduction and the movement of pollen between plants, in addition to the dispersal of seeds, affects the genetic variation of populations. Restriction in pollen movement reduces genetic variation within populations, whilst increases in genetic variation (heterozygosity) are achieved by outcrossing (Raven, Evert and Curtis 1982). Sexual reproduction, as well as allowing the expression of genetic variation, results in the production of dispersal units (fruits and seeds) which permit colonization of "new" sites. However, many plants have a capacity for vegetative regrowth; while this may permit long term population maintenance without a requirement for sexual reproduction it rarely provides a dispersal

Generalist species

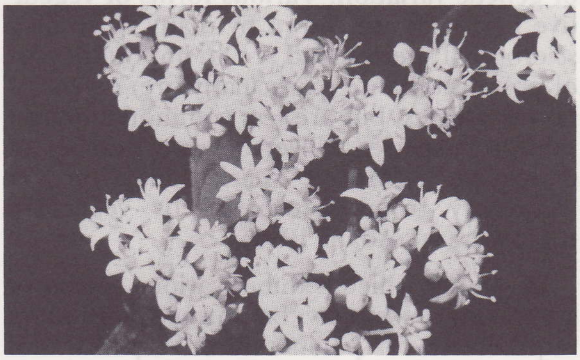

Figure 6. White flowered *Cuttsia viburnea* (Escalloniaceae) is a generalist, "entomophilous", small tree in subtropical rainforest pollinated by Diptera, Coleoptera, Hymenoptera and Thysanoptera. Diptera, Coleoptera and Hymenoptera are the principal pollination vectors of Australian tropical and subtropical rainforest trees with unspecialized, readily accessible, flowers.

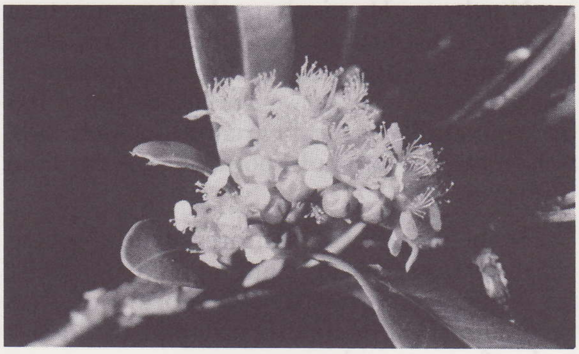

Figure 7. Yellow flowered *Tristaniopsis laurina* (Myrtaceae). *T. laurina* blossoms are visited by many bees, including Apidae, Halictidae, Colletidae-Euryglossinae, Colletidae-Hylaeinae, Colletidae-Colletinae, Megachilidae and trap-lining long-tongued Anthophoridae. There is no single bee-flower syndrome. "Bee-flowers" include specialized forms of various colours with nectaries deeply hidden in an extended perianth which are accessible to long-tongued and robust bees only, more shallow actinomorphic flowers with superior ovaries (e.g., *C. viburnea*) and unadapted "dish" or "cup" flowers (e.g., Myrtaceae), which are accessible to a wide range of unadapted or semi-adapted flower visitors.

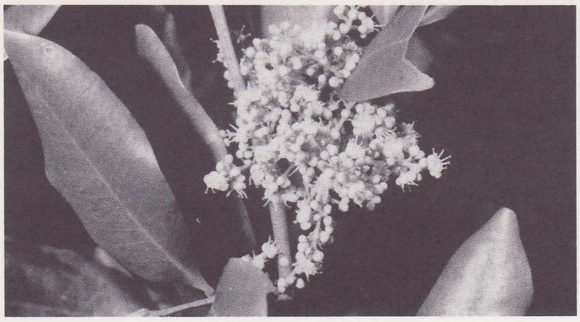

Figure 8. Male flowers of monoecious, sometimes dioecious, *Guioa semiglauca* (Sapindaceae) a pioneer species in subtropical rainforest. Fully dioecious and self incompatible species are obligate outcrossers and reproductive success of populations may be density dependent. Consequently, populations of obligate outcrossing plants, in fragmented rainforest habitats, are vulnerable to local extinction. This is because the reduction in population size and the spatial isolation of individual plants can result in decreased fecundity levels, insufficient to sustain a viable population.

mechanism and does not permit the expression of genetic variation. Various forms of vegetative regrowth are shown by many Australian sclerophyll species, and are an important part of post-disturbance (particularly fire) regeneration strategies, but are less common amongst rainforest species. Nevertheless a number of Australian rainforest species may recover vigorously from disturbance by vegetative regrowth (see Adam 1992).

In plants which exhibit various forms of apomixis, seeds may be formed without a requirement for pollination. A dispersal unit is thus produced but genetic variation is limited. The first documented example of apomixis (via agamospermy) was from a widespread Australian subtropical rainforest tree (*Alchornea ilicifolia* — Euphorbiaceae) (see Briggs and Walters 1984). Obligatory apomixis in Northern Hemisphere herbaceous taxa results in distinctive clonal local populations, sometimes recognized taxonomically as microspecies, but as far as we are aware there has been no study of local variation in *Alchornea*, nor further reports of apomixis in Australian rainforest trees.

For the majority of rainforest species sexual reproduction (perhaps augmented by ability for vegetative regrowth) is the norm, and thus pollination will be a necessary part of the life cycle of most species.

Influence of Breeding Systems

Reproductively mature plants cannot move to find partners and pollination in flowering plants requires the transfer of pollen grains, by the agency of either biotic or abiotic vectors, from anthers to the stigma (Bertin 1989; Raven, Evert and Curtis 1982). The later germination and growth of the pollen tube and fertilization of ovules, although essential for successful reproduction, are processes separate from pollination.

The requirement for a pollination vector is dependent upon the breeding system of a plant species.

There are three main categories of breeding systems in plants (House 1985) represented by:

1. Obligate outcrossing species (e.g., dioecious and self-incompatible hermaphroditic species).
2. Self-compatible hermaphroditic, and facultative outcrossing species (e.g., monoecious, gynomonoecious, protandrous, protogynous spp.).
3. Facultative inbreeders (self-compatible and apomictic plants) (in some apomicts inbreeding is obligatory).

The majority of woody tropical rainforest plant species which have been studied have adaptations for outcrossing (Bawa 1982; Sands and House 1990; Augspurger 1980) although the rate of outcrossing in populations and fecundity levels in individuals may be dependent upon the density of trees in flower (House 1992, 1993; Murawski and Hamrick 1992). A reduction in population density and fecundity levels, due to habitat fragmentation and consequent increased distances between obligate outcrossed rainforest plants (e.g., *Neolitsea dealbata* — Lauraceae), may threaten the long-term viability of local populations (House 1993). Outcrossing is often obligatory (i.e., in dioecious species) and self-incompatibility in tropical trees, especially pioneer species, has been reported as widespread (Dayanandan, Attygalla, Abeygunasekera, Gunatilleke and Gunatill 1990; Perry and Starrett 1980; Hubbell 1979; Bawa 1974). Low or variable levels of self-compatibility may occur in otherwise outcrossing species (e.g., Bawa 1974, 1992; Carpenter 1976; Appanah 1982; Crome and Irvine 1986; Murawski, Hamrick, Hubbell and Foster 1990; James and Knox 1993; Gross 1993; Proenca and Gibbs 1994) and this may result in some successful pollinations where cross pollination is unpredictable or pollinators are absent. Self-compatibility, however, may result in reduced offspring vigour and survivorship (Bertin 1989). Environmental conditions may affect the degree of self-compatibility, for example, many tree species in neotropical montane forests are self-compatible (Bawa 1990). The frequently cold and wet montane climates, which limit pollinator activity, may explain this preponderance of self-compatibility.

Dioecy (where male and female flowers occur on separate plants) is a mechanism which promotes outcrossing. House (1985, 1989, 1992, 1993) has studied pollination in north Queensland tropical rainforest populations of the dioecious *Diospyros pentamera* (Ebenaceae), *Litsea leefeana* and *Neolitsea dealbata* (Lauraceae). These species also occur in subtropical rainforest of southern Queensland and New South Wales. House compared population flowering synchrony, effective plant pollinator populations, and pollen loads being transferred between staminate (male) and pistillate (female) trees of the three species. The majority of anthophilous insects trapped (predominantly Diptera, Hymenoptera and Coleoptera) were between 3–6 mm long, with >74 per cent of the species and >67 per cent of individual insects carrying pollen ("home pollen") from the tree species at which they were collected. However, less than 8 per cent of individuals were found to be carrying home-pollen exclusively and House considered that none of the insects could be described as specialist pollinators. This absence of pollen load fidelity suggests that dioecy, as a sexual reproductive strategy, does not necessarily function to restrict pollen transport to host-specific pollinators and pollen flow between conspecific trees.

Russell-Smith and Lee (1992) found a significant number of dioecious species (19%, N = 16) amongst 84 tree species recorded from isolated monsoonal rainforest patches in the Northern Territory. The remaining species possessed bisexual or monoecious (cosexual) reproductive systems although the proportion of self-compatible species is unknown. We have found similar proportions of dioecious (18%, N = 26) and cosexual (82%, N = 116) reproductive systems in 142 tree species from lowland subtropical rainforests in the Manning Valley, lower north coast of New South Wales. Bawa (1990) gives percentages of dioecism as 21 per cent for Jamaican montane forest, 23 per cent for Costa Rican tropical lowland rainforest and 31 per cent for Venezualan montane forest. Ashton (1969) noted 26 per cent of trees, exceeding a 1 foot girth, in a mixed Sarawak dipterocarp forest to be dioecious. These figures suggest that around 20 per cent of species in different types of rainforest are dioecious, although why there should be this relatively similar proportion in rainforest floras with different histories and different contemporaneous environmental conditions is not clear.

There have been few studies of the pollination systems in subtropical rainforest species generally but as a broad generalization based on floral morphology it would appear that many species in New South Wales rainforest are either facultative or obligate outcrossers (see Harden 1990, 1991, 1992). Some species are dioecious, for example, *Euroschinus falcata* (Anacardiaceae), *Drypetes australasica* (Euphorbiaceae) and *Citronella moorei* (Icacinaceae) but descriptions of floral structure in Floras and handbooks may be inaccurate and convey misleading impressions as to possible breeding systems (for example, *Wilkiea huegeliana* — Monimiaceae — is reported by Floyd 1989, and Harden 1990, to be dioecious, but plants are frequently monoecious within populations we have investigated).

Amongst cosexual species outcrossing may be obligatory because of self-incompatibility. However, if self pollination can occur there is the possibility of seed set in the absence of pollination vectors, or where plant population size is so small so as not to attract pollinators. Data on the incidence of self-compatibility in rainforest trees is sparse; experimental bagging of developing flowers has indicated that a number of species in New South Wales subtropical rainforests are self-compatible (G. Williams, unpubl. data). Although bagging of flowers, in itself, does not provide a rigorous assessment of self-compatability it does provide an indication of "selfing" potential.

THE SPATIAL AND TEMPORAL STRUCTURE OF RAINFOREST

The effectiveness and availability of particular pollination vectors may be influenced by the structure of the forest. Rainforests are frequently structurally and floristically diverse (Primack and Hall 1992). There are exceptions to this general rule but for many tree species in complex rainforests mature individuals are scattered, posing difficulties for the transfer of pollen from one individual to another — if the vector is highly specialized how does it find individuals of a particular species? If the vector is a generalist then most pollen may be transported to non-conspecifics and thus be wasted.

In addition to the spatial discontinuity of resources (flowers) the temporal availability of resources in rainforest plant communities is normally "patchy", rather than constant and uniform (Newstrom, Frankie and Baker 1994). This temporal heterogeneity, or "mosaic", of resource availability will also influence pollination. Pollination vector populations may fluctuate in response to fluctuations in resource availability, but additionally, vector populations probably also fluctuate independently in response to various environmental factors. Rainforest trees can potentially counter fluctuations in vector availability by producing large numbers of flowers, in excess of those required to produce adequate seed set and by living a long time.

Phenology

Populations of many rainforest trees are highly synchronous in their flowering and this promotes conspecific pollen exchange. Flowering synchrony is thought to be strongly controlled by environmental conditions (Ashton, Givnish and Appanah 1988; Rathcke and Lacey 1985; Kinnaird 1992; Heideman 1989; Newstrom, Frankie and Baker 1994) and the ability to flower when potential pollinators are also abundant is generally considered to be strongly selected for, resulting in interspecific synchronization of flowering events in tropical rainforests (Sands and House 1990). However, there are many examples of species flowering outside periods of peak pollinator activity, and sequential or differential interspecific flowering, and this may be indicative of either selection pressure to compete for pollinators (Appanah 1990; Waser and Real 1979) or selection against hybridization (Stiles 1977; Cole 1981; Ashton 1969). Examples of mass-flowering subtropical trees in New South Wales flowering out of synchrony with peak pollinator densities include *Cupaniopsis anacardioides* (Sapindaceae), *Mischocarpus pyriformis* (Sapindaceae), *Orites excelsa* (Proteaceae), *Polyosma cunninghamii* (Escalloniaceae), *Doryphora sassafras* (Cunoniaceae) and *Geijera salicifolia* (Rutaceae). These generally flower during cooler months when the diversity (species richness) of pollinators is reduced and when individual populations of pollinators are also less numerous.

There can be considerable variation in the flowering patterns of rainforest trees and these patterns can be expressed heterogeneously by populations and individuals (Newstrom, Frankie and Baker 1994). Kinnaird (1992) observed marked spatial and temporal variation in the flowering schedules of East African riverine trees with flowering apparently triggered by low river levels rather than local reductions in rainfall. Appanah (1990) noted periodic but regular flowering species, trees that predictably flower annually, and supra-annually flowering trees in lowland dipterocarp rainforests (dominated by Dipterocarpaceae) in Malaysia. Many neotropical tree species flower each year (Bawa and Ng 1990), although Murawski, Hamrick, Hubbell and Foster (1990) observed variation in both the number of trees flowering, and the numbers of flowers produced on individual trees each year, in a population of the annually flowering neotropical *Cavanillesia platanifolia* (Bombacaceae). Continuous flowering in the strict sense, however, is uncommon and those rainforest trees that do flower over extended periods, or continuously, need to partition flowers and developing fruit so that pollination and dispersal functions do not interfere with each other. In the continuously flowering individuals of the lowland Central American tree *Muntingia calabura* (Elaeocarpaceae), the elongation and erection of the pedicel raises the flower buds above branches where they are pollinated by bees. Later, the developing fruit are lowered, concealed from predators below leaves, and finally dispersed by bats (Webb 1984). For the majority of woody rainforest flowering plants the possibility of interference between pollination and dispersal vectors does not arise because fruit maturation and dispersal occur after the cessation of flowering (Webb 1984).

Patterns of flowering and leaf production in tropical rainforests are often indirectly related to rainfall (Heideman 1989; Stiles 1977; Frith and Frith 1985; Wolda 1978), although individual species' responses to the same environmental cue may differ so that patterns of leaf and flower production in closely related species (i.e., *Shorea* spp., Dayanandan, Attygalla, Abeygunasekera, Gunatilleke and Gunatill 1990) can be widely divergent. Other climatic factors may also influence flowering; in the temperate rainforests of Tasmania, delays in flowering of *Eucryphia lucida* and *Atherosperma moschatum* can be related to slightly lower temperatures in the growing season (Read 1989). Different species are likely to respond differentially to environmental cues so that year to year variation in flowering patterns are unlikely to be in phase for all species.

Life cycles of phytophagous insects are generally synchronized to the availability of food resources or lowered chemical defences or increases in palatability in foliage (Basset 1991; Lowman 1982; Williams 1993; Fischer and Kogan 1986), with flower and leaf production and adult insect emergence probably cued by similar environmental triggers. Although there may be a lag time in pollinator response to the availability of flowers (House 1989), in both neotropical lowland rainforests and tropical Queensland montane rainforest peaks in flowering trees and insect numbers generally coincide (Sands and House 1990). However, in Australian tropical and subtropical rainforest, and sclerophyllous communities dominated by Myrtaceae, mass flowering events are not always paralleled by high numbers and diversity of insects (G. Williams, pers. obs.). This suggests that at least some entomophilous pollination systems may be pollinator, rather than resource limited in some years. Unreliability in the presence of pollinators may act as selection pressure in favour of self-compatibility and/or broad flexibility in potential pollinators. For long lived rainforest trees there may not be strong selection in favour of frequent reproduction but in shorter lived pioneer species in Australian subtropical rainforest frequent flowering is usually predictable, suggesting that regularity of reproduction is favoured (or normal).

In Australian subtropical rainforest most tree species flower between October and March (Floyd 1989). There is, however, specific overlap within, and divergence from, this general flowering period. Most Myrtaceae flower (but at different amplitudes) annually although the timing of onset of flowering may vary between years. Flowering episodes in some species (e.g., *Acradenia euodiiformis* — Rutaceae, *Guioa semiglauca* — Sapindaceae, *Dysoxylum fraseranum* —Meliaceae) are punctuated by several years in which no or very few flowers are produced. Phenological patterns within families may vary, for example within the Rutaceae species flower unpredictably (e.g., *A. euodiiformis*), annually with relative constancy of flower crop (e.g., *Acronychia oblongifolia*), or generally flower annually but with frequent marked variation in numbers of flowers produced (e.g., *Acronychia imperforata*) (G. Williams, unpubl. data).

Two distinct flowering strategies were exhibited by the three species studied by House (1985) in north Queensland. *Neolitsea dealbata* and *Litsea leefeana* (Lauraceae) flowered for periods of approximately 3–4 and 4–5 weeks respectively. These flowering periods, although shorter than those in many tropical species (House 1985), are similar in length to those of many subtropical rainforest trees (G. Williams, unpubl. data), and highly synchronous flowering promotes conspecific pollen transfer. In contrast *Diospyros pentamera* (Ebenaceae) flowered more extensively for over 15 weeks.

The Length of Flowering Life

Other factors which will be important to pollination in Australian subtropical (and tropical) rainforest trees are the length of life of individual flowers, the pattern of opening of flowers within inflorescences, and positioning of inflorescences. Even when individual flowers are inconspicuous their massing within inflorescences may make spectacular displays, while the length of time inflorescences are displayed may determine whether or not a particular pollinator becomes conditioned to visiting a species.

The longevity (the period between opening and senescence) of individual rainforest flowers has only rarely been investigated (Stratton 1989) although the life span of flowers could have a strong selective influence on pollinator visits and could affect the reproductive energy budget of the plant. There is a general correlation of increased flower longevity with increased altitude. Longevity is greater in more mesic habitats (see Primack 1985; Stratton 1989) but ecological differences between adjoining communities, whilst sufficient to alter floristic composition, do not necessarily alter mean floral longevity (MFL) (Stratton 1989). Stratton (1989, and references therein) summarized factors which may influence floral longevity, with factors tending to promote longer flower life including pollinator scarcity and unpredictability of pollinator visitation (also see Bawa 1990), pollen limitation in plants with many ovules per flower requiring longer periods to achieve maximum seed set, and selection for male function in hermaphrodite flowers.

Stratton (1989) determined MFL for 110 plant species (35 families, 71 genera) in Costa Rican cloud forest and semi-deciduous forest and concluded that there are strong phylogenetic constraints at the family level which limit the evolution of flower longevity. Ecological differences between his study sites apparently did not influence mean floral longevity, although these were sufficient to alter floristic composition. Stratton found greater duration in dioecious female, rather than male, flowers and the female phase of dichogamous (bisexual) flowers, and hypothesized that "floral longevity is influenced primarily by female function".

Flowers in high altitude tropical forests last an average 2–8 days longer than those in tropical lowland rainforest; the longer life span Bawa (1990) considers to be consistent with the notion of unpredictability in pollination at higher altitudes. Flower longevity is also related to structure and harsh environments might select for "stronger" structure, size and form in flowers which, coincidentally, live longer. Australia has a number of localities, in both the tropics and subtropics, where there are continuous sequences of rainforest from lowland valleys to mountain tops. Studies of flower longevity and flowering behaviour along these gradients would be of considerable interest.

Forest Strata and Synusiae

Structural complexity (and floristic composition) at any one point in a forest varies, both horizontally and vertically, with the stage of the regeneration cycle (Adam 1992). Flowering behaviour and pollination requirements might therefore vary in a multidimensional spatial mosaic reflecting the regeneration cycle.

Recognition of distinct vertical layers (strata) in rainforest is often more in the eye of the beholder than real, but recognition of emergent, canopy and understorey layers may be a useful level of subdivision. In addition to strata, recognition of specialized synusiae may also be useful.

The patterns of flowering behaviour may differ between strata and synusiae in the one forest, and these different flowering patterns and the different microclimatic conditions may mean that different pollination mechanisms are favoured at different positions within the forest structure.

Ashton, Soepadmo and Yap (1977) recognized two stratified layers, or synusiae, in Malaysian lowland dipterocarp forests, within which flowers were produced and to which pollinators responded differentially. They divided the rainforest trees into those that held their flowers above the canopy, and a second synusia whose members flower within the foliage. Appanah (1990) added to these a combined cauliflorous and ramiflorous synusia and a final heterogenous grouping of shrubs and herbs. The former is arguably a refinement of the subcanopy synusia of Ashton, Soepadmo and Yap (1977) whilst the latter might find greater expression in successional, gap phase, openings. Flowering epiphytes could arbitarily fit into a number of synusiae or form a synusia of their own. However, the recognition of stratified synusiae adds a vertical dimension to pollinator and resource selection in the rainforest community to which insects obviously respond (e.g., Appanah, Willemstein and Marshall 1986; Perry and Starrett 1980; Elton 1973; Janzen 1971). It is in the below-canopy synusiae that many instances of close plant-pollinator mutualism have been reported (e.g., Thien 1980; Armstrong and Irvine 1989a, 1989b; Hamilton 1897; Irvine and Armstrong 1990; Young 1990, Williams 1993). However, pollinator responses to floral resources within synusiae also have a behavioural basis (Appanah 1990; Roubik 1989; Janzen 1971). Perry and Starrett (1980) noted that for neotropical lowland forests, approximate stability (fidelity of taxa to synusiae) in the distribution and type of pollinator exists between understorey and canopy and that this is reflected in flowering strategies. Pollination of understorey plants was dominated by insects exhibiting traplining syndromes (that is, pollinators undertook long range foraging of a relatively constant spatial and temporal pattern), while mass-flowering dominated the canopy layer. Perry and Starrett (1980) proposed that the two strategies are related to pollinator density and that energetics, the caloric reward and cost of foraging (see Kearns and Inouye 1993; Barth 1991; Roubik 1989; Matthews and Kitching 1984), probably serves as a causal mechanism determining the vertical distribution pattern of strategies. However, in the case of sparsely distributed rainforest plants traplining may provide a mechanism for pollination but the distribution of plants can be explained in many ways unrelated to pollinator requirements.

Although the plant members of various tropical forest synusiae possess broadly defined characteristics of floral morphology, colour and scent cues, structure, floral rewards and breeding systems (see Appanah 1981), the restriction of pollinators to the various strata is not necessarily obligate. Appanah (1990), for example, notes that, in S.E. Asia, cauliflorous trees may recruit pollinating beetles and bees from the understorey synusia and that bats and birds from the upper canopy layer descend to forage on ramiflorous *Durio malaccensis* and *Ganua* species (in Australian subtropical rainforest ramiflory is an uncommon strategy; *Rapanea howittiana, R. variabilis* — Myrsinaceae, are examples). Likewise, Augspurger (1980) found that canopy-foraging *Melipona* bees (Apidae) in Panamanian lowland rainforest descended to forage en masse on synchronously mass-flowering understorey shrubs. Under conditions of low understorey flower resources, however, *Melipona* bees only occasionally foraged in the understorey and mass-flowering of individual plants was required to initiate foraging responses by the whole bee colony.

VEGETATION HISTORY AND ITS INFLUENCE ON PLANT-POLLINATOR RELATIONSHIPS

For much of the Tertiary rainforest was the predominant vegetation over most of Australia. With the onset of drier conditions in the late Tertiary, rainforest retreated in the face of the spread of sclerophyll vegetation. During the Quaternary there have been substantial fluctuations in the extent of rainforest and even within what is now the most extensive contiguous rainforest in Australia (north-east Queensland) the rainforest was fragmented and greatly reduced in area during dry (glacial) periods (Adam 1987, 1992; Truswell 1990; Walker 1990). Although shared predispositions may have served to retain some plant-animal linkages, Walker (1990) suggests that fluctuations in the extent and nature of rainforests reduced opportunities for establishment or retention of complex interdependencies and strong co-evolutionary mutualisms.

Plants and pollinators participating in obligate pollination mutualisms will be at risk if they respond differently to climatic and environmental fluctuations over evolutionary time spans. Communities in which obligate mutualisms are abundant may therefore be sensitive to instability (Bawa 1990).

Over shorter time scales (decades and centuries) the spatial complexity of plant distribution in rainforest may be initiated by chance events of canopy disturbance, fortuitous seed dispersal and canopy establishment (Ashton 1969; Wheelwright and Orians 1982; Williams 1993). The resulting stochastic instability within the trophic structure in rainforest communities may further preclude the establishment and maintenance of tightly circumscribed plant-pollinator relationships.

In the light of this temporal variability in resource availability flexibility in the pollination strategy of rainforest plants may be a specialized adaptation rather than an indication of lack of specialization.

PLANT-POLLINATOR INTERACTIONS

Flowers of individual species in the rainforest are, from the viewpoint of the potential pollinator, frequently a resource which is variable in abundance in time and space (because of lack of synchrony in flowering between and within populations) (Newstrom, Frankie and Baker 1994). Whilst some species may flower each year, even though the intraseasonal length of flowering and the numbers of flowers produced may vary, flowering by regional populations of other species can be episodic with flowering events separated by several or more years. From ecological and evolutionary perspectives this distribution of resources suggests that opportunities for closely coadapted plant-pollinator relationships would be rare and that most pollination would be effected by vectors, which, although they might be specialized pollinators (in as much as they visit particular flower types, or have selective and efficient foraging patterns), are nevertheless not closely tied to particular plant species. In order to test this hypothesis it is necessary to identify the pollination vectors.

This is not an easy task and many statements regarding pollination are often generalized inferences drawn from floral structure and behaviour. Certain syndromes of floral characteristics have been correlated with particular modes of pollination. While a particular syndrome may not be an absolutely reliable indication of pollination mechanisms it does appear to provide a good indicator for identification of biotic vectors at a higher taxonomic level, but cannot indicate the specific identity of the agent. Examples of particular floral syndromes are discussed further under the heading "Pollination Syndromes".

Recognition of specific pollination syndromes requires identification of visitors to flowers, from direct observation or sampling, and assessment of the efficiency of transfer of pollen and subsequent fertilization. These latter two factors are difficult to assess without experimental manipulation and it is easy to reach misleading conclusions from data based on the abundance, frequency or "conspicuousness" of visitors (see Crome and Irvine 1986; Hopper 1980; Bullock 1994). In discussion of the dispersal of pollen by animal vectors a distinction is made between the capacity of the vector to transport pollen and its ability to transfer pollen, resulting in placement of pollen on an appropriate stigmatic surface (Faegri and van der Pijl 1979). Transport can be relatively easily assessed, transfer is much more difficult to demonstrate.

Factors Affecting Movement of Pollinators

Factors which influence the movement of pollinators between plants may be both biological and environmental.

Biological factors promoting pollen transfer between (both sparse and mass-flowering) conspecific plants include temporal nectar flow pulses between sexes in dioecious species (Appanah 1982), periodic asynchronous cessation of flowering in male trees (House 1985, 1989), increased female flower longevity (Armstrong and Irvine 1989a), nectar satiation-induced outcrossing (Schemske 1980), dilute nectars forcing pollinators (birds) to forage more widely to satisfy energy requirements, and thus promote outcrossing (Bolten and Feinsinger 1978), territory (resource) defense (Rausher and Fowler 1979), insect density-induced disturbance (Frankie, Opler and Bawa 1976) and disturbance by insectivorous birds that induce other pollinators to disperse between flowering plants (Gentry 1978).

Circadian rhythms (Saunders 1977) also, provide a daily "pulse cycle" to the activity patterns of pollinators on flowers, with the movements of diurnal, crepuscular and nocturnal species facilitating some level of intra- and inter-population carriage of pollen. An additional, largely overlooked, mechanism available to effect movement of pollen is the influence of insect pheromones. In relation to sexual aggregation pheromones attract males to conspecific females on flowering trees and the reproductively cued movement of males would be expected to result in transference of pollen within single trees and within tree populations. Such intra and inter-tree pollen transfer is probably significant at least in some anthophilous Coleoptera, especially Scarabaeidae-Melolonthinae, Scarabaeidae-Cetoniinae and Buprestidae-Stigmoderini (Williams and Williams 1983; Matthews and Kitching 1984; Bernhardt and Thien 1987). Marked adaptations to chemoreception in Coleoptera are seen in the presence of receptive sensilla and associated foveae (e.g., on antennomeres) (Barth 1991; Richards and Filewood 1990; Gardner 1989; Crowson 1981; Fischer and Kogan 1986). The sensilla of Coleoptera are differentiated into specialized receptors of organic substances and pheromones (Crowson 1981, and his references).

The physical environment can profoundly influence movements and activity of pollinators and anthophilous insects (Kevan and Baker 1983; Cruden 1972). Kevan and Baker (1983) review the effects of storms, cloudiness, wind, rain and humidity on foraging patterns of anthophilous fauna. Sun flecks, for example, may encourage greater rates of visitation to otherwise shaded understorey flowers or extend the foraging periodicity of crepuscular species. Cloudiness, by restricting movements of specialized or traplining pollinators may allow an increase in the contributions of geitonogamy (pollination through pollen transfer between flowers of the same plant), via more sedentary pollinators, over that of xenogamous pollination (through pollen transfer between flowers of different plants). Temperature can have considerable influence on pollinator systems, both through affecting the activity of insects and by altering the volatization of attractants and nectar flow and viscosity (Williams and Williams 1983; Heinrich and Raven 1972).

The energy balance of pollination systems has both a plant and animal component (Kevan and Baker 1983). Plant and pollinator communities are interacting systems in which plants compete for pollinators and pollinators compete for floral resources. Plant-pollinator mutualisms may represent an optimization of fecundity for both partners, plant and animal, and whilst pollination success entails an energy cost to the plant (in terms of nectar and/or pollen) (Pyke 1991; Kearns and Inouye 1993) there is also an inherent energy cost to the pollinator during foraging (Bell 1990; Roubik 1989). Pollination also entails a reproductive cost to pollinator populations. This is incurred through predation and loss of individuals during foraging movements. Predators of pollinators may themselves perform pollination.

For both obligate and facultative pollinators nectar is the most common recorded reward and there is general correlation between nectar production and composition and the energy requirements and foraging periodicity of the pollinators (Kevan and Baker 1983; Bertin 1989; Gould 1978; Scogin 1980). The daily pattern of nectar production in rainforest trees can vary and correlates generally with visitations from pollinators (Carpenter 1976; Sazima and Sazima 1977, 1978). Not all anthophilous insects are pollinators (Augspurger 1980; Roubik 1989), and they may feed upon floral resources in their various forms (i.e., nectar, stigmatic exudate, pollen, resin, waxes, amino acids, floral parts), without any identifiable reproductive benefit to the plant (Bertin 1989; Matthews and Kitching 1984; Williams 1993). These species have been referred to as "thieves", where feeding is non-destructive, and "robbers", where damage to plant structures accompanies feeding (Bertin 1989). Ants are classically considered to be nectar thieves and although their feeding activities do not damage floral structures the antibiotic secretions of ants (Harriss and Beattie 1991) are likely to disrupt or inhibit pollen germination and growth of pollen tubes (Holldobler and Wilson 1990), and so limit their effectiveness as pollinators.

Not all true pollinators will necessarily be equally effective; some may primarily transport pollen within the confines of single tree crowns or even single inflorescences (e.g., ants) while others may transport pollen to conspecific plants over moderate (Appanah, Willemstein and Marshall 1986) or greater distances (Janzen 1971; House 1992). Pollinator efficacy will also be influenced by its population frequency, specific foraging behaviour and the structural modifications, characteristics or adaptive specialization that physically permit pollen collection and carriage. The introduction of exotic flower visitors (e.g., *Apis mellifera*) or removal of plants to areas of cultivation (or remnant vegetation within cultivation zones), gardens or regions removed from their natural range may obscure pollination modes and pollinator relationships. Flowering plants that disperse over long distances to islands are likely to leave their usual pollinators behind (Kevan and Baker 1983) and the lack of pollinator diversity on remote islands may act "as a potent biotic filter to potential plant immigrants" (Elmqvist, Cox, Rainey and Pierson 1992).

Bertin (1989) emphasizes that whilst pollen represents a source of food to some flower visitors, to others its presence may be an encumbrance (for example impeding flight) or, at least, irrelevant, thus introducing the caveat that whilst visitors may function as pollinating agents, in many cases they are probably acting unwittingly, with pollination being achieved incidentally.

Pollination of Sparsely-flowering Species

Pollen flow between individuals of neotropical rainforest plants with low population densities may be facilitated by large bees (Euglossini) which Janzen (1971) suggested permitted continued existence of tree species at low frequencies within the community. Long distance foraging activity was termed "traplining" and Janzen (1971) considered it was important to plants because it could permit effective outcrossing between plants at low densities, only small amounts of reproductive energy need be committed (because large numbers of blossoms were not required to attract pollinators) and that plants could occupy shaded habitats and be relatively assured of pollination. Frankie, Opler and Bawa (1976) found that low frequency inter-tree movements by solitary bees, predominantly Anthophoridae, were sufficient to account for observed fruit set success in widely spaced, self-incompatible *Andira inermis* (Papilionaceae) trees in disturbed lowland dry forest in Costa Rica. Similar "traplining" patterns of host fidelity and repetitive foraging in the understorey of Australian subtropical rainforest and wet sclerophyll forest are exhibited by large solitary anthophorid bees (i.e., *Lestis, Amegilla*) (G. Williams, unpubl. data). Gross (1993) records the large anthophorid *Xylocopa* species near gressitti foraging in a traplining manner on flowers of the rainforest and wet sclerophyll forest pioneer shrub *Melastome affine* (Melastomataceae) in tropical Queensland.

How do traplining insects locate flowering plants? Williams and Dodson (1971) demonstrated that attraction to specific floral fragrances, rather than floral phenology or morphology, could serve to recruit pollinators and facilitate pollen transfer. Whether this is the entrainment mechanism for all traplining insects is unknown, but there is ample evidence that phytochemical stimuli direct and modify insect pollinator responses to floral resources (Papaj and Prokopy 1989; Kevan and Baker 1983; Barth 1991; Allsopp 1992; Allsopp and Cherry 1991; Bell 1990).

Pollination of Mass-flowering Species

Heinrich (1975) suggested that the peak-phase blossoming of mass-flowering trees could attract large numbers of pollinators which would deplete the energy resource and then move to other conspecific trees thus promoting outcrossing, which primarily took place during this peak flowering stage. This idea is refered to as the conditioning-depletion hypothesis. Carpenter (1976) suggested that outcrossing in red flowered forms of *Metrosideros collina* (Myrtaceae) in Hawaii took place in early and late phase flowering with self-pollination predominating in the peak phase of flower availability. Stephenson (1982) found for mass-flowering *Catalpa speciosa* (Bignoniaceae) from North America that outcrossing predominated in the late, nectar depleted, flowering phase and that a large proportion of the receptive flowers (58 and 67%, in his study plots) available in the peak flowering phase remained unpollinated, which suggested that the flowers had retained their nectar reward. Stephenson considered that early and peak phase flowering served to initially recruit and then to condition pollinators to that species, with inter-tree movements increasing as conditioned insects feed on the resource-diminishing, late phase *C. speciosa* trees.

In north Queensland populations of *Litsea leefeana, Neolitsea dealbata* and *Diospyros pentamera* the majority of insect movements initially occurred within single tree canopies during early flowering phase (House 1985). Since male trees began to flower 2–3 days earlier than females, inter-tree transport of pollen commenced prior to female trees becoming receptive (House 1985). House suggested this initially resulted in wasted reproductive effort (because flowering female trees were not yet available), in the early (male) population flowering phase, but at a later reproductive benefit of having pollen already mobilized at opening of female flowers.

In all three tree species insect numbers increased and greatest quantities of pollen were mobilized at peak periods of flower availability. However, the greatest transfer of pollen to pistillate trees took place towards the end of the flowering period suggesting resource depletion may induce interplant movement of the accumulated anthophilous insect population.

POLLINATION AND THE AUSTRALIAN FLORA

Armstrong (1979) provided a review of biotic pollination mechanisms and floral pollination syndromes in the Australian flora generally, while more recent papers (e.g., Armstrong, Powell and Richards 1982; Williams, Knox, Gilbert and Bernhardt 1982; Howell, Slater and Knox 1993; Adams and Lawson 1993) provide additional data on pollination, secondary presentation of pollen, reproductive strategies and evolution. Armstrong (1979) provided an overview of pollination studies and literature prior to 1979 and discussed major groups of pollination agents (insects, birds, mammals, etc.), floral morphology, nectar production and chemistry in relation to putative pollination syndromes, reproductive and recruitment adaptations by plants to pollination vectors, and offered suggestions for future research. He reviewed the entomological literature for records of Australian invertebrates feeding on (but not necessarily pollinating) flowers and listed 28, of the then 121 recognized families of Coleoptera, and 44 of the 87 families of Diptera as containing anthophilous taxa. Armstrong (1979) stated that the Australian bee fauna is exclusively anthophilous and considered, on the basis of available data, that the Apoidea constitute the most important group of invertebrate pollination agents. Barlow (1981) commented that in arid areas the incidence of bird pollination is greatly reduced, that pollination contributions by terrestrial mammals appear to be absent and that in entomophilous plants pollination by Diptera-Bombyliidae (in addition to that by bees) becomes more important. More recent studies of Australian tropical rainforest ecosystems indicate that many groups of insects contribute substantially to pollen transfer and reproductive success and that within both Australian tropical, and subtropical rainforest at higher latitudes, bee pollination may be less frequent or entirely absent (see Irvine and Armstrong 1990; House, 1985, 1989).

Armstrong (1979) noted the greater importance of birds and mammals, both flying and terrestrial, as pollination agents in Australian plant communities than in northern temperate zone forests (Sussman and Raven 1978; Bawa 1990). Although bird and mammal pollination is relatively well documented for Australian sclerophyllous communities, in other plant communities it may be highly seasonal, incidental to other feeding activities, localized, unreliable or absent.

Jones and Crome (1990) reviewed the pollination systems of Australian tropical rainforest plants. They list known and assumed pollinators, irrespective of efficiency, for nine species of rainforest plants: an aroid (*Alocasia macrorrhiza*); seven trees, including one palm (*Archontophoenix cunninghamiana, Eupomatia laurina, Myristica insipida, Syzygium tierneyanum, S. cormiflorum, Flindersia brayleyana, Alphitonia petriei*) and one root parasite (*Balanophora fungosa*). These are pollinated by insect and insect-bird-bat dominated pollinator guilds. Overall, beetle-fly pollinator guilds dominated the systems they reviewed.

Jones and Crome (1990) discussed the apparent "flexibility" (or lack of specificity) in the plant-pollinator relationship shown by several of the tree species stating that ability to achieve pollen transfer was related to the physical capacity of the pollinator rather than pollinator taxonomy and that pollinator loss from the community may be alleviated by recruiting from within a guild or community pool of alternatively available vectors. They predicted that broadly defined plant-pollinator relationships will be progressively found in Australian rainforests and that pollinator replacement and broader oligotropic (oligolectic) (in which pollinators visit related plant taxa only) and polytropic (polylectic) (visiting many plant taxa) relationships by pollinators will be the general rule; a prediction which can be supported from the existing pollination and insect ecology literature (e.g., Wheelwright and Orians 1982; Primack 1978; Matthews and Kitching 1984; Heinrich and Raven 1972). Heinrich and Raven (1972) indicate that tropical forest ecosystems tend to be dominated by generalist pollination strategies.

The scenario of a broad pollinator guild and flexibility in the pollination system mirrors findings about the fruit/seed disperser relationships of African (Gautier-Hion 1990) and Central American (Howe 1990) tropical forests (reviewed by Terborgh 1990) where few tree species appear to have tightly delimited (1:1) links with dispersal vectors, and where a broadly defined disperser guild exists allowing flexibility in the reproductive strategy should individual biotic dispersal agents be removed from the community.

However it should be stated that:

- "tolerance" in the flexibility of the breeding systems (the point beyond which breeding system mechanisms will begin to fail following fragmentation of plant and, or, pollinator populations) of Australian rainforest trees is largely untested (only a small number of species has been investigated);
- apparent "flexibility" within the pollinator guild or breeding system may be a disturbance-induced disharmonic state (where the perceived relationships are artifacts of past disturbance) or part of an evolutionary shift in pollination strategy (e.g., from insect to vertebrate; animal to wind dispersion of pollen) (Faegri and van der Pijl 1979), so that flexibility may be a transitional state, not a facultative adaptation.

The general conclusion from both the literature and our observations would be that the majority of outcrossing species in Australian subtropical rainforests are insect pollinated (though some species may be cryptically anemophilous, see Bullock 1994).

Sands and House (1990) recognize two broad reproductive strategies in tropical entomophilous woody plants:

1. The production of a large conspicuous flower crop which attracts relatively unspecialized and often taxonomically-divergent insects. In this system, distance between conspecific plants, and thus movement of pollen, may be small and seed (fruit) is characteristically produced from a small percentage of the flowers produced. The reproductive effort is channelled into attracting opportunistic pollinators (a high excess in flower production, often in combination with high abortion rates of developing fruit, is widespread amongst flowering plants (Bawa 1982; Montalvo and Ackerman 1987)).
2. The production of small, inconspicuous flowers over longer time periods which may be pollinated by vectors (e.g., bees) with memories enabling repeated foraging patterns, often in spatially disjunct plant populations. This type of flowering has been recorded from Malaysian, Costa Rican and north Queensland rainforests and fruit number set often matches the numbers of flowers produced.

Pollination in Australian Myrtaceae

The Myrtaceae are an important element in the Australian flora and the diversity and dominance of Myrtaceae in many Australian plant communities are features which distinguish Australian vegetation from that elsewhere in the world. The dry-fruited Leptospermoideae (including *Eucalyptus, Melaleuca* and *Leptospermum*) are the major canopy dominants in sclerophyll forest, woodland and shrublands (Boland, Brooker, Chippendale, Hall, Hyland, Johnston, Kleinig and Turner 1984). Some elements of the Leptospermoideae are also important in subtropical rainforests (e.g., *Backhousia, Tristaniopsis*) and wet sclerophyll forest/rainforest transitions (e.g., *Lophostemon*). The fleshy fruited Myrtoideae (e.g., *Rhodomyrtus, Acmena, Syzygium*) include many species that occur in Australian tropical and subtropical rainforests, although the Myrtoideae have been relatively unsuccessful in colonizing fire prone habitats.

It is believed that the sclerophyll members of the Leptospermoideae have evolved from rainforest ancestors although the details of the separation of rainforest and sclerophyll elements in the flora remain obscure (Adam 1992; Barlow 1981; Briggs and Johnson 1979).

The reproductive biology of Australian Myrtaceae has been recently reviewed by Beardsell, O'Brien, Williams, Knox and Calder (1993) but despite the great economic importance of the family their pollination is poorly studied. Pollination of *Eucalyptus* spp. in northern Australia by large pteropodid flying-foxes is recorded by McCoy (1990) (see also Eby 1991). Ornithophily has arisen in several genera and is found throughout the ecological range of the family (Briggs and Johnson 1979). Entomophilous, characteristically small-flowered species, are also found through this ecological range and in New South Wales lowland subtropical rainforest pollination of fleshy fruited *Acmena smithii, Rhodomyrtus psidioides, Waterhousea floribunda* and dry fruited *Tristaniopsis laurina* is primarily achieved by small Hymenoptera, Coleoptera and Brachycera (G. Williams, unpubl. data). Proenca and Gibbs (1994) record six genera (*Eugenia, Siphoneugena, Blepharocalyx, Campomanesia, Myrcia* and *Psidium*) of Brazilian Myrtaceae as being bee pollinated.

In rainforests, the inflorescence of myrtaceous genera may be massed (e.g., *Backhousia,* some *Syzygium* species) or less conspicuous, often with large, single unmassed flowers (e.g., *Austromyrtus*, some *Syzygium* species). Ramiflorous and cauliflorous positioning of flowers (e.g., in *Syzygium cormiflorum*), and associated large, fleshy, animal-dispersed zoochorous fruit is exhibited by a number of species reflecting selection influences from both pollinators and dispersers.

The pollination ecology of two tropical Australian *Syzygium* species has been investigated. Hopper (1980) records 45 species of nectarivorous animals from *S. tierneyanum* and on the basis of observed abundance and foraging behaviour considered honeyeaters (Meliphagidae) and hawkmoths (Sphingidae) to be the most important pollinators, although honey bees were the most numerous flower visitors observed.

Pollination and the breeding system in *Syzygium cormiflorum* was examined by Crome and Irvine (1986). Although xenogamous, *S. cormiflorum* exhibited autogamous pollination success rates from 10 to 32 per cent. This degree of self-compatibility confers resilience in the absence of major pollinators (Crome and Irvine 1986). In *S. cormiflorum*, birds, insects and particularly blossom bats, were effective pollinators. Bats, either *Macroglossus minimus* (as *M. logochilus*) or *Syconycteris australis* (Crome and Irvine did not positively identify the species), and possibly large moths (Noctuidae and Sphingidae) accounted for 55 per cent of successful pollinations.

Syzygium cormiflorum can be compared with *S. syzygiodes* studied by Lack and Kevan (1984) from the lowland rainforests in Sulawesi (Celebes). These are forests of lower diversity than the dipterocarp dominated rainforests of the Sunda Shelf and the Malaysian peninsula. Trees are synchronous in flowering and populations flower over a period of 4–5 weeks. *Syzygium syzygioides* was strongly self-incompatible, with pollination success being insect visit-limited, in contrast to *S. cormiflorum*. Pollinators were recruited from a guild of short-tongued unspecialized insects with observed behaviour patterns indicating little promotion of outcrossing. Lack and Kevan did not record any visits to flowers by vetebrates (although Sulawesi has a rich bat fauna) and suggested the reproductive biology of the species seemed to be adapted to a species-poor community where specialization would be disadvantageous, suggesting that unspecialized entomophily is an adaptive reproductive strategy in mass-flowering trees in rainforest with depauperate pollinator guilds (Lack and Kevan 1984).

POLLINATION SYNDROMES

Although there are instances of observations of flower morphology resulting in incorrect inferences of pollination mode (Keller and Armbruster 1989; Kirk 1988b; Bullock 1994), broad correlations between floral structure and pollination vectors have permitted the recognition of pollination syndromes, allowing the broad groups of putative pollinators to be infered from the structure of flowers (Proctor and Yeo 1975; Sazima and Sazima 1978; Faegri and van der Pijl 1979; Bertin 1989). Morphological pollination syndromes may be correlated with phytochemical syndromes (Scogin 1980; Williams and Dodson 1971; Kirk 1985a) and in some cases with daily patterns of nectar production.

However, characterization of a particular plant species as a representative of single pollination syndrome may obscure wider plant-pollinator relationships. Kirk (1988b) stressed that members of several taxonomically and ethologically divergent animal groups may pollinate a particular plant species. Neither the most conspicuous flower visitors nor those which appear morphologically the best adapted to the flowers they visit are necessarily the most efficient pollinators (Kirk 1988b; House 1985). In addition, pollination relationships need not be symmetrical. Thus, for example, while certain beetles may only visit flowers with the cantharophilous (beetle pollinated) morphological syndrome, a flower from that syndrome might be visited by, and pollinated by, organisms from a range of taxonomic groups.

The differences between some described pollination syndromes are slight and thus in the course of evolution, only small changes to floral structure might have been required to result in a change of pollination vector, as has been shown by Kress (1985) in the case of *Heliconia* species (Heliconiaceae), which are pollinated in the Solomon Islands by nocturnal bats, but are primarily pollinated by hummingbirds in South America. Additionally, pollination may be achieved by both abiotic and biotic means; for example, Sharma, Koul and Koul (1993) record wind and insects as the principal pollination agents of *Plantago* spp. (Plantaginaceae).

Pollination syndromes are defined and discussed in detail in Faegri and van der Pijl (1979) but are discussed here because, in the absence of specific studies, they may permit an estimation of likely pollinators in Australia rainforests.

Anemophily

Anemophily (wind pollination) is the most common form of abiotic pollination and many dioecious rainforest plants thought to be pollinated by small insects may also be facultatively wind pollinated (Bullock 1994). Anemophily offers a release from the requirement to flower during periods of insect abundance and so anemophilous species need not conform to phenological patterns of entomophilous, or otherwise biotically pollinated plants within the community, although Kaul, Abbe and Abbe (1986) note that anemophily is possibly ineffective in seasons of high or unremitting rain. Size of individual pollen grains also influences pollen dispersal and the ability of the stigma to ensnare them (Kearns and Inouye 1993; Sharma, Koul and Koul 1993; Faegri, Iversen, Kaland and Krzywinski 1992). Small pollen grains potentially disperse over longer distances but may be less efficiently trapped by the stigma.

Although wind pollination has been considered to be rare in rainforest, its extent has been poorly investigated (Bullock 1994; Bawa and Crisp 1980) and may be more common than presently believed. Anemophily is reported in Malaysian, African and South American Moraceae, Central American Arecaceae and Urticaceae (Bawa and Crisp 1980; Milton 1991) and Malaysian Fagaceae (Bawa and Crisp 1980; Kaul *et al.* 1986). Bullock (1994) records anemophily in dioecious tree species of Achatocarpaceae, Amaranthaceae, Anacardiaceae, Capparaceae, Euphorbiaceae, Flacourtiaceae, Julianaceae, Moraceae, Nyctaginaceae, Oleaceae, Opiliaceae, Rutaceae and Urticaceae from a single neotropical deciduous-semideciduous forest site in Mexico and suggests that wind pollination may be common in plant species previously thought pollinated by small generalist insects. Pollination by wind may also occur in Australian *Malaisia scandens* (Moraceae) and *Streblus brunonianus* (Moraceae) (Williams and Adam 1993) and thus, anemophily in the Moraceae (excluding *Ficus*) appears to be widespread. Using the presence of variously branched, plumose, filamentous and enlarged stigma morphologies recorded from anemophilous flowers (see Bullock 1994) as a guide, anemophily might be predicted in species of Australian rainforest Euphorbiaceae (e.g., *Omalanthus populifolius, Croton verreauxii*). Arecaceae were considered to be anemophilous but pollination by insects also has now been widely reported (Uhl and Moore 1977; Barford, Henderson and Balslev 1987; Anderson, Overal and Henderson 1988; Schatz 1990). Although the spatial and structural complexity of tropical and subtropical rainforests, as well as climatic conditions, may preclude the wider expression of anemophilous pollination strategies, a greater prevalence of anemophily may be anticipated in certain rainforest formations. In Australia these might include floristically and structurally simple inland and maritime vine thickets, *Backhousia sciadophora* (Myrtaceae) dominated dry rainforests (which structurally can resemble *Eucalyptus* dominated dry sclerophyll forest) (Williams 1993) and *Nothofagus* (Nothofagaceae) dominated cool temperate rainforest. Anemophilous pollination strategies might also be more commonly encountered in successional gap phase communities because the initial, relatively open structure favours more efficient (less impeded) pollen transfer to conspecific plants.

General Entomophily

In generally entomophilous blossoms (e.g., *Cuttsia viburnea* — Escalloniaceae [Fig. 6], *Tristianiopsis laurina* — Myrtaceae [Fig. 7], *Guioa semiglauca* — Sapindaceae [Fig. 8]) there is little depth effect in the perianth, the flowers are actinomorphic (radially symetrical) and open, and the sepals are often reduced. Stamens are usually free and reduced in size and daily nectar volumes may be small (Kearns and Inouye 1993).

General unspecialized entomophilous pollination has been recorded in a diverse range of plant taxa from a wide range of Australian rainforest types. These include *Eucryphia lucida* and *E. milliganii* in Tasmanian cool temperate rainforest (Ettershank and Ettershank 1990), and *Flindersia brayleyana, Alphitonia petriei* (Irvine and Armstrong 1988, 1990), *Diospyros pentamera, Litsea leefeana* and *Neolitsea dealbata* (House 1985, 1989, 1992, 1993) in Queensland tropical rainforest. Unspecialized entomophilous floral sydromes are also possessed by many New Zealand species, which Primack (1978) considered an adaptation to highly variable, ecologically unspecialized insect pollinators that dominated the available pollinator assemblage.

This wide occurrence of pollination by small unspecialized insects does not accord with the depauperate pollinator guild hypothesis advanced by Lack and Kevan (1984), which suggests that selection for unspecialized flowers is an adaptation to low species richness of potential pollinators.

Neither does it support the suggestion of Bawa (1990) that general entomophily is favoured by lower temperatures. The unspecialized entomophilous syndrome should not necessarily be construed as a primitive or conservative feature. By recruiting pollinators from a wide range of small insects, plants may be buffered from environmental fluctuations and the spatial and temporal fluctuations of pollinators (see Herrera 1988) which might affect the abundance of individual species but not the total insect population. As Bertin (1989) observed; "The success of a system is judged not by its degree of specialization, but by its persistence in evolutionary time".

Beetles — Cantharophily

Irvine and Armstrong (1990) reviewed the contributions of adult beetles to the pollination ecology of tropical forests with particular reference to Australia. Beetles are recorded as pollinators in an ecologically diverse, phylogenetically heterogeneous assemblage of plants that, in rainforest, occupy canopy, subcanopy and field strata (Williams 1993; Hamilton 1897; Irvine and Armstrong 1988, 1990; Thien 1980; Young 1990; House 1989; Schatz 1990; Anderson, Overal and Henderson 1988; Forster 1989; Barford, Henderson and Balslev 1987; Monteith 1986). Irvine and Armstrong (1990) suggested beetle pollination may be more important in Australian tropical rainforest than in tropical America and that differences in pollinator prominence may reflect differences in dominance of flower types in north Queensland and the Neotropics. In Queensland tropical rainforest populations of the dioecious tree *Diospyros pentamera* beetles, compared with other anthophilous insects, carried the largest pollen loads and moved more frequently between staminate (male) and pistillate (female) trees, and are thought to be the main pollinators (House 1985). Armstrong and Irvine (1989b) record small weevils and nitidulid beetles as pollinators of the dioecious Queensland subcanopy rainforest tree *Myristica insipida* (Myristicaceae).

The cantharophilous syndrome encompasses a broad range of floral structures (see Irvine and Armstrong 1988, 1990; Armstrong and Irvine 1989a, 1989b), which overlap with those of a number of flower syndromes, and includes plant species whose flowers emit sweet fragrances or strong fruity or aminoid odours.

This emission of strong odour, either sweet or fetid, appears to be the unifying theme linking the structurally and phylogenetically diverse range of plants from which beetles have been reported as pollinators (Irvine and Armstrong 1988, 1990; House 1989; Armstrong and Irvine 1990; Monteith 1986). This correlates with the marked development of olfactory senses in Coleoptera (Gardner 1989; Crowson 1981; Lawrence and Britton 1991; Fuchs 1974; Britton 1970). A number of beetle-pollinated plants volatize odours by raising the temperature of flowers (e.g., Schatz 1990; Young 1990). Monteith (1986) notes that peak heat production in the dung beetle pollinated arum lilly *Typhonium brownii* (Araceae) may reach 15.5°C above ambient. Several groups of Coleoptera show pronounced responses to heat (e.g., *Merimna, Diadoxus* — Buprestidae) but the possible direct function of increased temperature as an attractant to pollinators has not been investigated.

Beetles are thought generally to lack colour vision (Crowson 1981) but whilst individual flowers may lack visual attractions (Faegri and van der Pijl 1979) cantharophilous plants may also produce large, massed inflorescences that cumulatively establish a strong visual stimulus.

Crowson (1981) divides modern floricolous Coleoptera into two groups; a larger group of families that visit flowers solely for adult feeding and a second group whose larvae develop in flowers and fruits. Some families (i.e., Nitidulidae — which are pollinators of Australian subtropical rainforest *Hibiscus splendens* and *H. heterophyllus* — Malvaceae, and *Alocasia brisbanensis* — Araceae, Williams 1993) are represented in both groups. The former group, however, possesses taxa with marked adaptations to the floricolous habit, including specialized mouthparts for nectar feeding, prolongation of the front part of the head (frontoclypeus) and long and dorsally inserted antennae. Mouthpart morphology of nectar-feeding Coleoptera is discussed by Crowson (1981), Selander (1957), Gardner (1989), Britton (1970), Lawrence and Britton (1991), and Fuchs (1974).

In flower-frequenting beetles the orthognathous (perpendicular) positioning of the mouthparts is considered to be the original or primitive state and is characteristic of the many phyllophagous forms, in which also, the mandibles are well developed for chewing. The orthognathic condition of the mouthparts is indicative of unadapted (dystropic) and poorly adapted (allotropic) beetles (Faegri and van der Pijl 1979). Prognathous mouthparts characterize specialized floricolous Coleoptera in which the mouthparts are acuminate and produced parallel to the body axis and in which the maxillary palps, the galae and laciniae, are specialized for nectar-feeding (Fuchs 1974). There is no clear phylogenetic deliniation of orthognathous and prognathous forms; the determining influence being largely an ecological one. The prognathic condition, with prolonged mouthparts and acumination of the frontoclypeus, reaches extreme development in nectar-feeding Buprestidae — Stigmoderini (Gardner 1989) (in particular the *producta* spp. group of *Castiarina*), Buprestidae — Anthaxiini (*Curis*) (Bellamy 1986) and Cerambycidae — Calliprasonini (McKeown 1947) and Cerambycidae — Psilomorphini (Scambler 1993). Prolongation of mouthparts is also characteristic of flower-visiting Rhipiphoridae, Tenebrionidae — Alleculinae, Meloidae, Oedemeridae, Cantharidae, Mordellidae, Scarabaeidae — Cetoniinae and Scarabaeidae — Sericini. These appear to be eutropic, fully adapted, obligate blossom visitors. In Australia these anthophilous Coleoptera are characteristically associated with sclerophyllous and mesic adapted Myrtaceae (Hawkeswood 1978, 1981a, 1982; Hiller 1990; Webb 1986a, 1986b; Williams and Williams 1983).

It has been suggested that beetles are inefficient pollinators, because they possess generally "smooth" bodies unsuited to pollen carriage (Bertin 1989; Barth 1991), but this argument is invalid. The integument of anthophilous Coleoptera and, in particular the anteroventral and frontal regions, possess many structures capable of carrying large pollen loads. These include antennal and frontal cavities, setal clusters, foveal pits and finer punctation (in the Meligethinae-Nitidulidae mandibular dorsal cavities may carry pollen (Crowson 1988, 1990; Endrody-Younga and Crowson 1986)), and behaviour and flight orientation is well developed in many anthophilous Coleoptera so that transfer of pollen between plants is facilitated.

Caution is needed in the interpretation of findings of pollen removal by beetles (and other vectors). Ramsay (1988) found that whilst staphylinids in a sclerophyllous *Banksia menziesii* (Proteaceae) population removed large amounts of pollen, they deposited none on the stigmata.

The evolutionary development of a cantharophilous syndrome was reviewed by Irvine and Armstrong (1988), drawing upon the earlier work of Gottsberger (1974, 1977). Beetle pollination is often associated with primitive families of angiosperms (e.g., Magnoliaceae, Annonaceae, Eupomatiaceae). However, Bernhardt and Thien (1987) consider that beetle pollination in living relictual plants "appears too specialized to represent an ancestral condition" and that flowers pollinated exclusively by beetles represent a derived condition. Protogyny is often associated with cantharophily and many "primitive" or evolutionarily conservative angiosperms are protogynous. Schatz (1990) suggests this may have obviated the need to evolve self-incompatibility systems but protogyny within individual trees does not preclude self-pollination via geitonogamy.

Diels (1916) and Gottsberger (1974, 1977) suggested that beetles were the first pollinators of angiosperms. Bernhardt and Thien (1987) and Grinfeld (1975) suggest that beetles formed part of a proto-pollinating, pollen-feeding insect guild that later began visiting early angiosperms. There is a close relationship between neotropical Arecaceae (which are now considered doubtfully primitive) and the beetle families Nitidulidae and Curculionidae (in the pantropical Derelomini) (Anderson, Overal and Henderson 1988; Barford, Henderson and Balslev 1987; Uhl and Moore 1977). Derelomine weevils (*?Amorphoidea linospadicis*) are also known from flowers of the subtropical understorey palm *Linospadix monostachyus* (Williams, unpubl. data). Both families are represented in late Jurassic fossil deposits (Crowson 1981) and if the geologically early derivation of Arecaceae (Uhl and Moore 1977) can be maintained then the evolutionary relationship between Nitidulidae and Curculionidae and palms is a long one.

There has been historical controversy over the precursor polarity of the beetle feeding state (herbivory vs. pollen feeding), with implications as to the mode of pollination and evolution in primitive angiosperms (Irvine and Armstrong 1990). However, the pollen feeding association of curculionid weevils with cycads, and their apparent role in pollen transfer (Norstog, Stevenson and Niklas 1986; Ornduff 1989, 1990; Forster, Machin, Mound and Wilson 1994; Chadwick 1993), lend support to the pre-existing selection for pollen feeding and facultative pollination by beetles prior to the late Cretaceous radiation of the Magnoliopsida (sensu Harden 1990). Overlooked in the literature has been the evolutionary transition of predacious Coleoptera (e.g., Cantharidae, Melyridae, Staphylinidae and Cleridae) to pollen feeding (Crowson 1981), providing evidence of the acquisition of a pollinivorous (pollen feeding) habit independent of a pathway predicated upon transitional herbivory.

Elleschodes and *Eupomatia*

The classical beetle pollination studies in Australia rainforest ecology are those on the understorey shrub, or small tree, *Eupomatia laurina* (Eupomatiaceae) (Figs 3, 4, 5) (Hamilton 1897; Hotchkiss 1958; Endress 1984; Armstrong and Irvine 1990; Irvine and Armstrong 1990). *Eupomatia laurina* provides one of the few described examples of close linkages between plant and pollinator amongst Australian rainforest plants.

Eupomatia laurina is distributed from eastern Victoria to north Queensland (Williams *et al.* 1984) and altitudinally from approximately sea level to >1 000 m. It is not restricted to rainforest and can occur as a common understorey small tree in wet sclerophyll forest. It reproduces vigorously vegetatively and is one of the relatively few rainforest species in Australia which can recover from even severe bushfire damage (P. Adam, G. Williams, pers. obs.).

The Eupomatiaceae retain floral structures thought to characterize the hypothetical primitive angiosperm condition (Thien 1980). Ancestral angiosperm groups are now extinct, but there is a concentration of relictual, evolutionarily conservative plants in the southwestern Pacific Basin (Thien 1980).

In *E. laurina* large, white waxy flowers, with strong fruity odours are borne singly, or sometimes in small groups. Flowers do not possess a perianth but are formed by basally united stamens and large fleshy staminodes that collectively form the synandrium. The synandria absciss approximately 14–30 hours after anthesis (Irvine and Armstrong 1990).

Individual subtropical *E. laurina* populations show between — site asynchronous flowering cycles but within individual subtropical populations flowering is broadly synchronous with intra-population flowering of individual trees extending over approximately 2–3 weeks. Flowers on single plants open synchronously between approximately 0330–0630 hours. Although small numbers of flowers may open several days prior to and following the main flowering episode, >500 flowers, on a single tree, may open synchronously (G. Williams, unpubl. data).

Throughout its range, *E. laurina* is pollinated by a single weevil genus, *Elleschodes* (Armstrong and Irvine 1990). Hotchkiss (1958) noted that an *Elleschodes* sp., collected at Bellingen, New South Wales, is also associated with *Eupomatia bennettii* and *Elleschodes* weevils (which are not conspecific with *E. hamiltoni* but are apparently closely related to it) have been collected in flowers of *E. bennettii* at Terania Creek in far northeast New South Wales (H. and N. Nicholson, pers. obs.). The north Queensland *Elleschodes* spp. are undescribed but southern *E. laurina* populations are pollinated by *Elleschodes hamiltoni*. Adult weevils leave the flower at dusk through the dehiscing protogynous anthers and move to flowers opening at dawn the next day fertilizing stigmas as they move around on the floor of the floral chamber without damaging the stigmatic surface. The synchronization of flower anthesis and abscission of the synandrium facilitates outcrossing (Irvine and Armstrong 1990; Hotchkiss 1958).

Armstrong and Irvine (1990) investigated the staminode function in this florally-conservative, apparently adaptively successful, angiosperm. They found that enveloping staminodia acted as protective screens for adult weevils against predators (although their putative predator, the green tree ant *Oecophylla smaragdina*, does not occur south of central coastal Queensland, Hacobian 1992), apical tips functioned as food sources, staminodia enhanced visual display and carried osmophores for the production of attractant odours and produced sticky exudates that facilitated carriage of heavy pollen loads (300+ grains) on individual weevils. These features have been proposed as characteristics of the floral morphology of relic Magnoliales (Endress 1984; Armstrong and Irvine 1990).

In terms of beetle larval development the abscissing floral synandrium provides a food substrate removed from the developing gynoecium (Armstrong and Irvine 1990). However, little is known of the life history of *Elleschodes*. Zimmerman (in Armstrong and Irvine 1990) noted the presence of large fat bodies in north Queensland *Elleschodes* species. This suggests that the weevils may be able to remain inactive within the soil profile awaiting onset of suitable environmental conditions or emergence cues. Williams and Adam (unpubl. data) observed that subtropical *E. hamiltoni* populations in New South

Wales pupated in the soil for eight to 18 days and under laboratory conditions emerged over a 10 day period (in which >98 per cent of adults emerged within the first 4 days). Such generally synchronous emergence, if coinciding with *Eupomatia* flowering, would be advantageous in maximizing utilization (and consequent reproductive success) of the equally synchronized anthesis of the host plant population.

The original study of pollination and breeding system in *Eupomatia laurina* (Hamilton 1897) was undertaken in the Illawarra district of southern coastal New South Wales, although earlier reports of *Eupomatia* flowering had been made by Robert Brown in 1814 and by Bennett in 1860. Hamilton observed the rapid exit and dropping responses of weevils when disturbed. This is a predator-avoidance mechanism acting independently of Armstrong and Irvine's (1990) postulated protection function of the staminodia. Similar "drop-escape" responses are found in a number of beetle families and are characteristic of many phyllophagous Buprestidae, Chrysomelidae and Curculionidae. Hamilton also described the pollen loads on weevil tarsomeres, antennomeres and setae, the shedding of the fused petal and sepal cap (forming a eucalypt-like operculum) on anthesis (Fig. 3) and the abscission of the synandrium.

Diptera — Myophily, Sapromyophily

Faegri and van der Pijl (1979) and Bertin (1989) characterise the fly blossom syndrome as one of unspecialized, actinomorphic flowers with "no depth effect", in which the colours are generally light or dull and with nectar guides frequently present. Odours are absent or imperceptible (at least to humans) and nectar is easily obtainable. Sexual organs are well exposed. Armstrong (1979) also included short, tubular blossoms (e.g., *Leucopogon* — Epacridaceae) with relatively inaccessible nectaries and concealed stamens in the general myophilous flower syndrome.

The greatest diversity of Diptera occur on accessible unspecialized blossoms and there is a correlation between short proboscis length and unspecialized shallow blossoms, and increasingly longer proboscis length and specialized tubular blossoms (Armstrong 1979), although species with long probosces are also able to take exposed nectar in shallow blossoms (Holloway 1976).

Visitation and pollination by flies, often in combination with pollination by beetles (Lloyd and Wells 1992) and Hymenoptera, forms a dominating trait amongst unspecialized entomophilous rainforest plants (Jones and Crome 1990; House 1985, 1989). Primarily myophilous pollination is recorded in tropical *Aristolochia* and *Rafflesia* (Bawa 1990) and *Drimys* (Gottsberger 1974; Thien 1980). Sciarid and chloropid flies are considered putative pollinators of Australian *Marsdenia cymulosa* (Asclepiadaceae) (Forster 1992b). Lloyd and Wells (1992) record chironomid flies as common visitors to female flowers of New Zealand *Pseudowintera colorata* (Winteraceae). Whilst fly pollination is well known for tropical herbs, Ashton (1969) considered that fly pollination in trees was rare but pollination by small Diptera (in combination with Hymenoptera and Coleoptera) of dioecious *Neolitsea dealbata, Litsea leefeana* and *Diospyros pentamera* trees in Queensland tropical rainforest has been demonstrated by House (1985, 1989).

Armstrong (1979) reviewed contributions by flies to the pollination of Australian plants generally. Armstrong (1979) suggested that for pollination Brachycera, which includes at least 30 families with anthophilous taxa, are the most important suborder of flies. However, Syrphidae, "hoverflies", and particularly the Bombyliidae, "bee flies" (both of which are generally adaptively specialized flower feeders), are not as common on Australian mass-flowering rainforest trees as they are on sclerophyll species. In comparison with syrphids and bombyliids, Phoridae, Lauxaniidae, Tephritidae, Chloropidae, Drosophilidae and other small unspecialized brachyceran flies are well represented on the flowers of subtropical rainforest trees.

The second dipteran suborder, Nematocera, in Australia includes at least 12 families containing anthophilous species but most nematocerans possess short mouthparts and are generally restricted to shallow flowers of open, readily accessible, structure or small tubular blossoms. Specialized pollination relationships exist between Nematocera and terrestrial Australian orchids (e.g., *Pterostylis, Acianthus* and *Corybas*) (Kevan and Baker 1983; Matthews and Kitching 1984; Armstrong 1979) and although these are principally non-rainforest genera several species occur in subtropical or cool temperate rainforests, or associated ecotones.

Small Diptera, prone to desiccation, are better represented in mesic habitats, or more moist biotopes, than in sclerophyllous communities, and so Diptera — Nematocera, in terms of diversity, are probably better represented amongst the anthophilous fauna of rainforest understoreys. The pollen carrying capacity of small flies is limited but this may be partially compensated for by their abundance. Their low energy demands are met by the minute quantities of nectar or pollen produced by small flowers, allowing smaller-sized Diptera to occupy a particular ecological niche — that of the small, inconspicuous flower.

In addition to the specialized nectar and pollen-feeding Diptera there is a second, sapromyophilous, group of flies that is attracted to flowers by deceit. These flies are attracted by fetid odours that stimulate feeding or oviposition instincts (Faegri and van der Pijl 1979). Such flies, typically Sepsidae, Calliphoridae, Sarcophagidae and Tachinidae, are poorly adapted, allotropic species that only derive part of a mixed diet from blossoms. In Australian subtropical rainforest flies from these families are common on the fetid-sweet flowers of *Alphitonia excelsa*.

Faegri and van der Pijl (1979) and Bertin (1989) distinguish a separate sapromyophilous flower syndrome from general myophily. Sapromyophilous flowers are often greenish, purple or brown with no nectar guides but frequently with dark spots and motile hairs, capable of movement, or appendages. There is generally no nectar attractant but sapromyophilous flowers produce strong fetid odours. In addition, the sexual organs are generally concealed within the blossom. Sapromyophilous flowers, often with "fly trap blossoms" (formed by a modified perianth or leaf spathe), occur in families such as Aristolochiaceae, Araceae, Asclepiadaceae, Burmanniaceae, Hydnoraceae, Orchidaceae, Rafflesiaceae, Sterculiaceae and Taccaceae (Faegri and van der Pijl 1979; Armstrong 1979) in addition to more primitive taxa (i.e., Annonaceae) and such blossoms might be a secondary development in the pollination ecology of plants, developing from an earlier established syndrome (e.g., cantharophily) (Faegri and van der Pijl 1979).

Hymenoptera

Pollination contributions by Hymenoptera are both diverse and extensive and occur over a wide range of plant taxa, plant communities and geographical and climatic regions. Australian records were reviewed by Armstrong (1979). The influence on, and importance of, floral colours to bees is discussed by Barth (1991), Kevan and Baker (1983), Raven, Evert and Curtis (1982), Roubik 1989, Bertin (1989) and Menzel and Shmida (1993).

Wasps — Sphecophily

There appears to be no specific syndrome of sphecophily, as termed by Armstrong (1979), in Australia with wasps (and "saw flies") being associated with diverse blossom types. These include highly modified flowers, such as those in the Orchidaceae (Matthews and Kitching 1984) and Moraceae (Matthews and Kitching 1984; Wiebes 1979; Boucek 1988), and relatively unspecialized, readily accessible actinomorphic flowers with both highly fragrant, sweet or fetid odours (e.g., *Tristaniopsis laurina* — Myrtaceae, *Alphitonia excelsa* — Rhamnaceae, G. Williams, unpubl. data). Heithaus (1979) records wasps taking nectar from bat-pollinated plants. Comparative studies of wasp diversity between neotropical and northern temperate habitats (Heithaus 1979) indicate greater diversity in the former and overlap with bees in resource utilization.

The term "wasp" encompasses a heterogeneous assemblage of both "primitive", unspecialized and highly evolved families. Mouthparts may be adapted to prey capture and excision from the pupal cell or host, or in higher, aculeate groups (e.g., Vespoidea, Sphecoidea), there are tube-like modifications to the mouthparts (particularly prolongation and development of the glossae, paraglossae and prementum) to allow nectar to be sucked up (Naumann 1991; Riek 1970; Faegri and van der Pijl 1979; Williams and Adam, in press). In Sphecidae-Bembicini the morphological distinction between "wasps" and bees (Apoidea) becomes fine and somewhat arbitrary and although sphecids are regular and frequent flower visitors, they retain predacious habits. Although wasps may be attracted to flowers for nectar, some wasps in otherwise nectar-seeking families (e.g., Sphecidae, Scoliidae), frequent flowers to capture true pollinators.

Some documented instances of wasp pollination are highly specialized and apparently highly evolved plant-wasp pollination relationships are documented for *Ficus* (Moraceae) — Agaonidae, Orchidaceae — Ichneumonidae, Orchidaceae — Scoliidae and Orchidaceae — Thynninae (Tiphiidae) (Armstrong 1979, and his references). Pollination by wasps in Australian rainforest plant taxa, other than for several species of *Ficus*, is poorly known although records exist for higher wasp families (e.g., Tiphiidae, Vespidae, Scoliidae) visiting Mimosaceae, Myrtaceae, Loranthaceae, Orchidaceae, Proteaceae, Sapindaceae, Goodeniaceae, Gyrostemonaceae and Lamiaceae in Australian non-rainforest communities (Armstrong 1979; Hawkeswood

1981b; Houston 1984; Brown 1987, 1989a, 1989b; Webb 1989; Inouye and Pyke 1988). Armstrong (1979) also note Pergidae (Symphyta) associated with Campanulaceae, Myrtaceae and Rutaceae blossoms. Vithanage and Ironside (1986) recorded pollination of *Macadamia* (Proteaceae) by the scoliid *Campsomeris tasmaniensis*. Vespoidea and Sphecoidea wasps are recorded visiting flowers of Ebenaceae and Lauraceae (House 1985) in tropical Queensland rainforest, and Anacardiaceae, Apocynaceae, Arecaceae, Cunoniaceae, Ebenaceae, Escalloniaceae, Myrtaceae, Rhamnaceae, Sapindaceae and Vitaceae species in lowland subtropical rainforest remnants of New South Wales (Williams and Adam, in press; G. Williams, unpubl. data).

Fig-Fig Wasp Mutualism

The genus *Ficus* (Moraceae) (e.g., *Ficus coronata* [Fig. 1]) contains approximately 900 species (Janzen 1979a) and is dependent on Agaonidae-Agaoninae (Chalcidoidea) wasps (as defined by Boucek 1988) for pollination (Compton, Ross and Thornton 1994). Fig wasps may disperse over distances greater than 100 km (Pemberton 1934, cited in Compton, Ross and Thornton 1994), this dispersal capability potentially enabling the wasps to reach and pollinate hyperdispersed fig populations.

Volatile chemicals in figs are thought to attract fig wasps (Bronstein 1988). Boucek (1988), on the basis of the analysis of morphological characters, considers that the true fig wasps developed from primitive prototorymid seed-eaters and that these pre-agaonids eventually co-evolved with different species of figs, developing different morphologies in relationship to differences in syconia morphology (e.g., thickness of syconia walls, size of fig).

The pollination system in figs has been well described by Weibes (1963, 1979) and Boucek (1988). Each fig, however, has to pay a reproductive price for pollination. Janzen (1979b) found that for Costa Rican *Ficus* spp., seed loss (due to development of agaonid larvae) per fig was not less than 25 per cent, 75 per cent seed loss was commonplace, and that a generalized mean sample loss was probably 55 per cent which he then considered as the reproductive (offspring) price for successful outcrossing.

Fig-agaonid wasp relationships are generally considered host-specific, although breakdown in pollinator specificity is noted by Ware and Compton (1992) and Kjellberg, Gouyon, Ibrahim, Raymond and Valdeyron (1987). The Australian fig wasps are still poorly known (Boucek 1988; Naumann 1991) and few fig species have been investigated (Matthews and Kitching 1984). Current Australian agaonid-fig records include *Pleistodontes froggatti (Ficus macrophylla)* (Riek 1970; Armstrong 1979), *P. froggatti (F. rubiginosa), P. imperialis (F. macrophylla)* and *Kradibiella* sp. *(F. coronata)* (Matthews and Kitching 1984). Shared agaonid records for *Ficus rubiginosa* and *F. macrophylla* indicate lack of complete host specificity.

Ants — Myrmecophily

Although ants are numerically abundant in many communities their role and function in effecting pollination has been discounted or questioned (Armstrong 1979; Barrows 1977; Faegri and van der Pijl 1979; Williams and Williams 1983; Harriss and Beattie 1991; Peakall, Beattie and James 1987; Kevan and Baker 1983). Limitations to ant pollination have been considered to be the small size of many flower visiting species, which purportedly precludes contact with stigma or stamens, the smoothness of the body integument, spatially or behaviourally-restricted foraging patterns which restrict pollen transfer, and the pollinicidal nature of metapleural glandular secretions that may interfere with pollen germination or stigma function. However, there are records of ants pollinating plants (Hickman 1974; Bertin 1989; Armstrong 1979; Peakall, Beattie and James 1987) although some plants may possess morphological or chemical defenses that deter ant visits (Schubart and Anderson 1978; Faegri and van der Pijl 1979; Guerrant and Fiedler 1981). Guerrant and Fiedler (1981) demonstrated the general palatability of floral nectar to ants. This would appear to discount suggestions (Janzen 1977) of chemically unpalatable nectar substances militating against ant visitation to flowers in lowland tropical habitats.

Tentative ant pollination syndromes have been postulated (Bertin 1989; Holldobler and Wilson 1990; Hickman 1974). Features of plants possibly pollinated by ants are suggested to include high plant density, small inconspicuous flowers borne near the ground, sessile flowers with low nectar volumes and few concurrently open flowers, low ovule number (thus requiring smaller levels of pollen transfer), small amounts of dry sticky pollen, interdigitation of branches from adjacent plants and a warm, dry habitat. However, Peakall, Beattie and James (1987) demonstrated that ant pollination is not confined to plants with these traits suggesting that "plant form is not the determining factor in the evolution of ant pollination". Rather, pollination by ants may require the absence of pollinicidal secretions, or the evolution of plant mechanisms that allow the avoidance of these secretions (Peakall, Beattie and James 1987).

It is generally established that the secretions from the metapleural glands function as powerful antiseptics against body surface and nest micro-organisms and as a defense against predators (Holldobler and Wilson 1990). Possession of metapleural glands is widespread in Formicidae and characterizes the family throughout their phylogenetic history. However, in some *Camponotus, Dendromyrmex, Oecophylla* and *Polyrhachis* the metapleural glands are secondarily atrophied or lost (Holldobler and Wilson 1990). These genera include many arboreal species (with *Polyrhachis* being particularly well represented in subtropical littoral rainforest of northern New South Wales, G. Williams, unpubl. data) but there do not appear to be any data that demonstrate correlation of absence (or modification in function) of the metapleural gland to ability to act as pollinators in the anthophilous or nectarivorous ant fauna.

Bees — Melittophily

While many species of bees are highly efficient foragers they possess a wide range of foraging behaviour and patterns and varying degrees of specialization as flower visitors and potential pollinators (Roubik 1989; Gross 1993).

The foraging behaviour, and specialization in the diversity of plant taxa visited, varies between opportunistic, polytropic (polylectic) bees that visit many species of plants, to oligotropic (oligolectic) or monotropic (monolectic) bees that are restricted in the range of flowers visited (Roubik 1989; Faegri and van der Pijl 1979). Consequently, there is no single bee-specific flower syndrome. Specialized, highly adapted, traplining and eusocial bees visit zygomorphic, robust flowers that have the nectaries hidden and pollen often presented as discrete pollinia units rather than individual, if sticky, grains. Such flowers are rarely massed in large inflorescences, often have deep tube-like corollas, are brightly coloured yellow or blue, usually with prominent or distinct nectar guides, the odours are obvious and fragrant, they produce nectar in moderate quantities, sexual organs are concealed with few stamens and many ovules per ovary (Faegri and van der Pijl 1979). The depth effect of the perianth partitions the type of bees that can forage successfully, so long and short-tongued species tend to utilize flowers of different depths (Real 1981; see also Kato, Matsumoto and Kato 1993), although robust bees are able to break through the base of the corolla to reach otherwise inaccessible nectaries (Roubik 1989). Opportunistic, polytropic bees (and some more highly adapted species) commonly visit flowers with general entomophilous traits of open actinomorphic form, with shallow "dish-like" corollas (coloured white or dull), often in massed paniculate inflorescences, with small to moderate quantities of nectar and sweet odours.

Bees collect both nectar, pollen and occasionally resin (Armbruster and Webster 1979), (although these are not the only floral rewards offered to anthophilous insects, Roubik 1989; Buchmann and Buchmann 1981; Armstrong and Irvine 1990) but are not exclusively anthophilous (Roubik 1982, records instances of necrophagy). Bees will collect from plants without nectar rewards (Petanidou and Ellis 1993; Gross 1993; Adam, Fisher and Anderson 1987; Bullock, Martinez del Rio and Ayala 1989; Snow and Roubik 1987; Bernhardt and Thien 1987; Buchmann and Buchmann 1981). However, the pollen collected in the specialized corbiculae of social Apidae is not available for pollination (House 1989) and some reduction in pollen viability may occur, although this is not necessarily significant, when pollen comes into contact with the body integument (Harriss and Beattie 1991). Not all bees collect and carry pollen among specialized scopal hairs. Australian Colletidae — Hylaeinae and Colletidae — Euryglossinae carry pollen in the crop (Michener and Houston 1991; Exley, Schneider and Daniels 1993), and may possess specialized setal brush structures (e.g., on the fore tarsi) with which pollen is swept into the mouth, as in female Hylaeinae (Houston 1975).

The role of bees in tropical ecosystems has been extensively reviewed by Roubik (1989). Many bees are important pollinators but, nevertheless, their role, function and behaviour varies in response to climate, latitude, vegetation structure and aggregation and size of individual plants (Dylewska 1993; Seeley 1983; Heithaus 1979; Bawa 1990;

Cruden 1972; Bullock, Martinez del Rio and Ayala 1989) and seasonal abundance (Roubik and Ackerman 1987). Daily foraging patterns are also temperature dependent (Real 1981; Dylewska 1993). Bee pollination dominates in biotically pollinated temperate plants and in neotropical lowland rainforest the majority of trees in many common families (e.g., Burseraceae, Euphorbiaceae, Clusiaceae, Fabaceae, Flacourtiaceae, Lecythidaceae, Melastomataceae, Orchidaceae, Sapotaceae), and particularly canopy trees, are bee pollinated (Bawa 1990). Highly eusocial bee species comprise a larger proportion of neotropical faunas than temperate ones (Heithaus 1979), though the species richness of bees in the tropics is apparently less than that of warm temperate regions (Roubik 1989). The ecological diversity of tropical bees, however, is much greater than that recorded from elsewhere (Roubik 1989).

In Australia, the primitive Colletidae are well represented (Michener 1970; Exley, Schneider and Daniels 1993) and occur on a heterogeneous range of plant taxa throughout much of the continent (Armstrong 1979). Most Colletidae, however, are oligolectic on Myrtaceae (Cardale 1993; see food plant records in Exley 1968a-e, 1975) and thus constitute, with Buprestidae-Coleoptera (see Barker 1979, 1986; Bellamy 1986, and references therein) (and some other Coleoptera), an anthophilous, taxonomically-distinct insect group characteristic of this distinctive family of Australian plants. *Homalictus* spp. (Apoidea-Halictidae) also exhibit a preference for Myrtaceae (Walker 1986). Oligolectic bees show little foraging constancy within Myrtaceae and forage on whatever plants in that family are in blossom (Armstrong 1979; Michener and Houston 1991), however, oligolectic bees may not be true pollinators but rather be depletors of nectar (Armstrong 1979; Steiner 1985; Bullock 1994). Colletidae appear to be implicated in the pollination of few primitive angiosperms, and the majority of bee pollination in primitive flowering plants appears to depend upon more advanced Apidae (Bernhardt and Thien 1987). Bee pollination in primitive plant taxa probably evolved from more generally entomophilous systems (Bernhardt and Thien 1987) and an evolution to bee specificity has been demonstrated in divergent, allied, entomophilous plant taxa (Ashton 1969, citing Bateman 1951).

The majority of Australian bees are solitary (Cardale 1993), although the Euglossini-Apidae (Armbruster and Webster 1979; Ackerman 1983; Roubik 1989), which are principally solitary (although some are communal or quasisocial, Ackerman 1983), are absent. In Australia, the highly social Apidae are represented by *Trigona* (some species have recently been placed in the genus *Austroplebeia*, T. Heard, pers. comm.) whose distribution is tropical-subtropical, and the introduced "honey bee" *Apis mellifera*, represented by several races. *Apis mellifera* may compete with Australian native bees and other insects for floral resources (Paton 1993; Sugden and Pyke 1991; Pyke and Balzer 1985). Although *A. mellifera* has been recorded from Australian tropical and subtropical rainforest trees (House 1989; Hopper 1980; G. Williams, unpubl. data) the function and impact of introduced honey bees in Australian rainforests has not been well studied. Paton (1993) has pointed out that there may be both positive as well as negative impacts of honey bees and cautions against assuming that honey bees are necessarily a major problem for managers of reserves. Australian *Trigona* spp. are efficient pollinators of *Macadamia integrifolia* (Proteaceae) in plantations (Heard 1993) but all Apidae are not necessarily effective pollinators. Steiner (1985) found *Euglossa* spp. to be nectar thieves on Panamanian *Drymonia serrulata* (Gesneriaceae) whilst abundant *Trigona* spp. on *Prockia crucis* (Flacourtiaceae), probably pollinated only rarely (Bullock, Martinez del Rio and Ayala 1989). Gross (1993) considered that *Trigona carbonaria* was a pollen "robber" of the pioneer shrub *Melastoma affine* in tropical Queensland. Dodkin (1987) noted the high rate of resource depletion of *Heliconia psittacorum* by "parasitic" *Trigona trinidensis*. However, Appanah (1982) and Appanah, Willenstein and Marshall (1986) record *Trigona* spp. pollinating Malaysian rainforest trees, whilst Bernhardt and Thien (1987) cite automimetic attraction of trigonid bees by synchronously flowering, protogynous *Piper* (Piperaceae) and *Pothomorphe* (Piperaceae) flowers. McAlpine (1988) also records a *Trigona* species (questionably *T. carbonaria*) taking pollen from the spadix of *Alocasia brisbanensis* (as *A. macrorrhiza*) (Araceae) in south-east Queensland. Williams (1993) records *T. carbonaria* visiting *A. brisbanensis* in New South Wales lowland subtropical rainforest. Adams, Bartareau and Walker (1992) record *Trigona* bees as pollinators of Australian *Dendrobium*, *Cymbidium* and *Caladenia* orchids and as probable pollinators of *Sarcochilus moorei*.

There are differences of opinion as to the spatial distribution of bee pollination systems in tropical forests. Appanah (1981), Appanah, Willemstein and Marshall (1986), Ackerman (1983) and Augspurger (1980) regard bee pollination as a characteristic of shaded zones and understories, whilst Bawa (1990) states that pollination by medium size to large bees and small taxonomically diverse bees in tropical lowland rainforest primarily occurs in the canopy.

Foraging behaviour may be expressed laterally through horizontally layered forest strata or vertically in response to resource availability in either canopy or subcanopy synusiae. However, highly adaptive or specialized foraging behaviour does not automatically confer high levels of pollination and many bees, including highly developed eusocial species, may contribute little to reproductive success (Bullock 1994). In the neotropical tree *Prockia crucis* (Flacourtiaceae), for example, visitation is by a taxonomically and behaviourally diverse guild of bees but most of these are minor resource thieves and not pollinators (Bullock, Martinez del Rio and Ayala 1989). Additionally, none of the pollinators or thieves are specialists.

Nectar depletion in bee-visited plants also serves to diurnally partition the types of bees that will forage (Roubik 1989). Real (1981) found that in the Costa Rican rainforest vine *Ipomoea batatas* bees showed staggered visiting times with larger-sized species visiting early in the morning and late in the afternoon, during periods of nectar maxima, and smaller bees visiting during the interim period when nectar availability was at a minimum. Willmer (1988) demonstrated that nectar concentration is a potentially major determinant of bee foraging activity and that physiological information can be useful in deciphering insect-plant co-evolutionary patterns.

Lepidoptera — (Butterflies — Psychophily, Moths — Phalaenophily)

Psychophilous and phalaenophilous flower syndromes are discussed by Faegri and van der Pijl (1979). In moth-blossoms attraction by olfactory cues is more significant than in those attractive to butterflies and the fragrances of such flowers are strong (Faegri and van der Pijl 1979) and may be accompanied by pronounced periodicity of odour production.

In both butterfly and moth-pollinated blossoms the floral tube is often very long and slender (Bertin 1989) and the nectar produced is less viscous than in "bee" flowers. The length of the floral tube and the length of the lepidopteran proboscis are inter-dependent limiting factors for both the plant and the types of lepidopterans that can effectively reach nectar resources. In the majority of Lepidoptera food uptake can only occur via the proboscis and so, nectar viscosity (dilute solutions exhibit increased capillarity) is a limiting factor to Lepidoptera resource utilization (Faegri and van der Pijl 1979). Some species of micropterigid moths apparently feed directly on pollen (Faegri and van der Pijl 1979; Kevan and Baker 1983). A wide range of amino acids has been found in the nectar of many flowers at which Lepidoptera feed (Armstrong 1979).

The role of colour as an attractant in nocturnal, moth-pollinated flowers is still undetermined (Faegri and van der Pijl 1979) but in plants pollinated, or at least visited, by diurnally active butterflies, blossom colours may be vivid but are also commonly white. There are some marked divergences from the generalized Lepidoptera-pollinated syndrome and a number of phalaenophilous, specifically sphingophilous (hawk moth pollinated), blossoms are nectarless, lack corolla tubes, produce no scent and are not white (Haber and Frankie 1989; Haber 1984).

There is some similarity in syndrome between bird-pollinated, ornithophilous flowers, and flowers visited by diurnally-active lepidopteran pollinators (Faegri and van der Pijl 1979). Direct competition is known between diurnally-active hawk-moths (Sphingidae) and hummingbirds (Trochilidae) and pollination by both hawkmoths and birds occurs in a number of plant taxa (Baker 1961; Ashton 1969). Ashton (1969) considers that phalaenophilous rainforest trees are not necessarily vector-specific and can be promiscuous, attracting moths, birds, bats and bees. Haber and Frankie (1989) reported visitations by hawkmoths to many species of neotropical dry forest plants adapted for other pollination vectors (e.g., bats, hummingbirds, bees) in addition to hawkmoth flowers in which the floral tube or perianth was shorter than the length of the moth proboscis.

There are significant behavioural differences that distinguish the pollination contributions of moths (Heterocera) and butterflies (Rhopalocera). Generally, the flight activity of moths is crepuscular or nocturnal (Common 1970, 1990) whilst that of butterflies is almost exclusively diurnal. There are exceptions and in Australian tropical ecosystems *Alcides zodiaca* (Uraniidae), *Nyctemera amica* (Arctiidae) and *Macroglossum micaceum* and

M. nubilum (Sphingidae), and in subtropical lowland littoral rainforests *Amata* species (Arctiidae), are common diurnal flower frequenting moths (Common 1990; Hopper 1980; G. Williams, unpubl. data). Although numerous nocturnally active moths visit the flowers of subtropical rainforest trees their contribution to plant pollination is unknown.

Behavioural divergence exists within the moths with some groups, most markedly the Sphingidae, hovering during feeding and others (e.g., Noctuidae, Amatidae) alighting and clambering over individual blossoms and massed inflorescences. This difference in behaviour directs placement of pollen. In hovering species the pollen is deposited on the proboscis or nototribically, but in those species which alight, sternotribic pollen deposition occurs.

Pollination by hawkmoths (sphingophily) has been more extensively investigated in tropical forests than has pollination by other moths and butterflies and their "hovering" method of flight is energetically very expensive (Nilsson, Jonsson, Ralison and Randrianjohany 1987). Food plant constancy is recorded in Sphingidae (Nilsson, Jonsson, Ralison and Randrianjohany 1987) and traplining behaviour is also known (Linhart and Mendenhall 1977).

Butterflies are very visible components of the insect faunas of tropical ecosystems but whilst they visit many brightly coloured and taxonomically unrelated flowers, butterfly pollination systems are among the least studied in tropical rainforests (Bawa 1990). Many *Eugenia* spp. (Myrtaceae) in Peninsular Malaysia are pollinated by danaid butterflies (Appanah 1990). Hopper (1980) recorded seven butterfly species on the related *Syzygium tierneyanum* in north Queensland, but House (1989) rarely trapped or observed Lepidoptera on dioecious *Litsea leefana, Neolitsea dealbata* (Lauraceae) or *Diospyros pentamera* (Ebenaceae). Cultivated *Hoya australis* (Asclepiadaceae) were found to be pollinated by the hesperiid butterfly *Ocybadistes walkerisothis* (Forster 1992a). Williams (1993) records butterflies as pollinators of the tree *Pararchidendron pruinosum* (Mimosaceae) and the vine *Parsonsia straminea* (Apocynaceae) in lowland subtropical rainforest of New South Wales.

Miscellaneous Insect Groups

Records for flower visitation by members of other Australian insect groups are given in Armstrong (1979) but their contribution to pollination is largely unknown. Collembola (springtails) have been recorded as pollen feeders from a variety of (mainly temperate and polar) plants (Kevan 1972, 1978). Pollen has been recorded from the gut of an Australian collembolan (P. Greenslade, pers. comm.).

Thysanoptera (thrips) have been recorded as pollinators in Malaysian dipterocarp forests (e.g., Appanah and Chan 1981; Appanah 1990), in Australasian Winteraceae (Bernhardt and Thien 1987; Thien 1980) and in *Mollinedia* (Monimiaceae) (Gottsberger 1977). The composition and concentration of floral scents and flower colour influence the attraction of thrips species to blossoms (Kirk 1985a).

Pollination by thrips may be more widespread than is generally realized (Kirk 1987). Kirk (1988a, 1988b) proposed a tentative thrips pollination syndrome (thripophily, Kirk 1988b) that included "white to yellow, sweet-scented flowers with compact floral structures . . ." and possibly nocturnal presentation of pollen to distinguish thripophilous flowers from bee flowers. To Kirk's thripophilous characters we add globose-urceolate blossoms (that provide enclosed brood sites for thrip eggs and larvae) (e.g., *Wilkiea huegelina* [Fig. 2]), not necessarily with an obvious fragrance, to accommodate thrips-pollinated Monimiaceae (*Mollinedia* Gottsberger 1977; *Wilkiea huegeliana* G. Williams and P. Adam, unpubl. data), Myrsinaceae (*Rapanea howittiana, R. variabilis*), Smilacaceae (*Smilax glyciphylla*), Arecaceae (*Linospadix monostachyus;* also pollinated by weevils) and Moraceae (*Maclura cochinchinensis*) (Williams 1993; G. Williams and P. Adam, unpubl. data). The monoecious subtropical shrub *Breynia oblongifolia* (Euphorbiaceae) also possesses flowers that agree with the syndrome of thripophily, but no thrips species, have as yet, been associated with flowers. Robinson (1991) reports that *Rapanea* (Myrsinaceae) is cleistogamous but this may be based upon a misinterpretation of floral structure. Although thrips are recorded as pollinators of several "primitive" angiosperms, they are only rarely associated with gymnosperms and are believed to have radiated to flowering plants from a plesiotypic or detritivorous habit (Mound 1991).

Thrips are widely recorded as pollen consumers. Kirk (1987) investigated the impact of thrip feeding on pollen grains of "kiwifruit" *Actinidia deliciosa* and "Paterson's Curse" *Echium plantagineum.* Feeding time was proportional to grain volume and was temperature-limited, daily feeding rates differed significantly between pollen types and daily consumption of pollen accounted for 0.2–0.7 per cent "of the average total pollen production of a flower per thrips per day". Kirk suggested that pollen damage by thrips could sometimes reduce crop yields or plant fitness but that pollen consumption by thrips may still be at a net plant reproductive benefit if thrips pollinate as well as consume.

Birds — Ornithophily

Specialized bird flowers are brightly coloured (e.g., red, red-yellow) and lack odour but contra to Bertin (1989) many ornithophilous blossoms possess perching or landing platforms (Armstrong 1979; Faegri and van der Pijl 1979). Recruitment to bird flowers is primarily visual and red is classically considered to be a bird-attracting colour (Proctor and Yeo 1975; Faegri and van der Pijl 1979). In the Costa Rican liana *Combretum farinosum* (Combretaceae), red flowers which produce very little nectar apparently serve as "flags" to attract pollinating hummingbirds to nectariferous green-coloured blossoms (Schemske 1980).

In fully bird-visitor adapted plants, visited by specialized (eutropic) birds, nectar is abundant and deeply held within the extended perianth. For such fully adapted plants, nectarivorous birds must be long-tongued and long-billed (Bertin 1989). In Hawaiian lobelioids (Campanulaceae) there is a correlation between length of the perianth tube and the beak length of the honeycreeper (Drepanididae) pollinators (Ashton 1969; Grant 1949) and such characteristics can serve as isolating mechanisms, promoting speciation among plant species.

Pollination by birds is widely reported in tropical rainforests and southern temperate regions (Ippolito and Armstrong 1993; Bawa 1990; Bertin 1989; Crome and Irvine 1986; Feinsinger, Swarm and Wolfe 1985; Seifert 1982; Hopper 1980; Toledo 1977; Carpenter 1976; Cruden 1972; Ashton 1969). Pollination systems involving birds in the Northern Hemisphere are poorly developed (Sussman and Raven 1978; Proctor and Yeo 1975). There is little fidelity or constancy by pollinivorous and nectivorous birds and most rainforest birds are polytropic or oligotropic in the range of plant taxa visited (Faegri and van der Pijl 1979).

Many rainforest bird species show intermediate degrees of specialization in their adaptation to flower visiting but in the neotropical hummingbirds (Trochilidae) and sugarbirds (Coerebidae), Hawaiian honey creepers (Drepanididae) and Old World-Australasian sunbirds (Nectariniidae) and honeyeaters (Meliphagidae) adaptations to utilizing blossoms as the main source of nutrients are more fully developed, although many are partly insectivorous (Toledo 1977). Trochilidae, Coerebidae and Drepanididae are absent from Australia, Nectariniidae are restricted to tropical Queensland (Pizzey 1982) and the Meliphagidae, whilst having radiated widely within Australian ecosystems (Turner 1982), are poorly represented in rainforests at higher latitudes (Adam 1987, 1992).

Ornithophily in the Australian flora, in a geological and evolutionary sense, is a relatively recent phenomenon (Armstrong 1979) and many types of putative ornithophilous blossoms show differential adaptation to entomophily and chiropterophily, in which ornithophily may be transitional.

In Australian plant communities generally, bright red colours in bird pollinated flowers are relatively infrequent (Armstrong 1979 and his references) but there are several Australian subtropical rainforest trees that possess floral characters that meet the criteria for putative bird-pollination syndromes (e.g., Dorrigo Waratah *Alloxylon pinnatum*, Silky Oak *Grevillea robusta*, Firewheel Tree *Stenocarpus sinuatus* — Proteaceae; Flame Tree *Brachychiton acerifolius* — Sterculiaceae, Bat's Wing Coral Tree *Erythrina vespertilio*, Black Bean *Castanospermum australe* — Fabaceae). These include radially symmetrical, semi-adapted actinomorphic blossoms, and more specialized bilaterally symmetrical, zygomorphic, blossoms. A number of trees occurring in Australian subtropical rainforests (e.g., *Syzygium moorei* — Myrtaceae, *Archidendron grandiflorum* — Mimosaceae) possess pink, brush-shaped flowers that suggest possible transition from insect to bird-pollination (or an adaptation to pollination by both).

A number of these species (e.g., *Brachychiton acerifolius*) are often characterised by highly dispersed populations with isolated individuals separated from conspecifics by many kilometers. This in itself might suggest that pollination is achieved by vectors, such as birds, that range over long distances allowing tree populations to exist at very low densities. However, many subtropical rainforest trees, that are not pollinated by vertebrates (e.g., *Endiandra discolor*), also occur at very low densities over large ranges. Therefore the spatial distribution and population density of rainforest plants may not necessarily provide clues to their pollination ecology.

The pollination ecology and breeding systems of Australian subtropical and warm temperate rainforest trees are largely unstudied. Birds play an important pollination role in Australian sclerophyllous heaths, woodlands and forests (Turner 1982), particularly in the pollination of *Blandfordia, Eucalyptus, Callistemon* and *Melaleuca* (Armstrong 1979; Turner 1982; Ford, Paton and Forde 1979). Contrasting their role in sclerophyllous vegetation, with the situation in rainforest, Adam (1987) noted that in the rainforests of New South Wales birds rarely feed on nectar and pollen and that the Meliphagidae, although a conspicuous element of Australian northern tropical forests and open temperate vegetation, are usually represented by a single species, *Meliphaga lewinii*, Lewin's Honeyeater. However, secondary growth (seral) subtropical rainforests, rainforest trees along forest margins and ecotones and species-poor rainforests may be able to recruit other meliphagids from adjoining sclerophyllous communities. Flower visitation by brush-tongued lorikeets (Loriidae) is primarily restricted to eucalypts occurring in the rainforest-wet sclerophyll forest interface but pollination by parrots apparently does not contribute greatly to pollination in southern Australian rainforests.

Bats — Chiropterophily

The floral syndromes characterising pollination by bats are well established (Faegri and van der Pijl 1979; Bawa 1990; Scogin 1980; Kress 1985) and orientation by bats to blossoms is by sight or smell (Kress 1985). Specialized bat flowers open at night, normally open for only a single night, are normally whitish in colour, and are rarely brightly coloured and possess strong, nocturnally-produced, musky, sometimes sweet, odours. (Kress 1985 notes the absence of strong odours in both neotropical and paleotropical *Heliconia* spp. (Heliconiaceae)). They produce large quantities of nectar nocturnally, and large amounts of pollen, are large-mouthed and have strong single flowers, or are "brush" flowers (as in Proteaceae, Myrtaceae, Capparaceae, Barringtoniaceae, etc.). In the Indonesian *Freycinetia insignis* (Pandanaceae) the food reward is in the form of large sugary bracts (Proctor and Yeo 1975). The positioning of bat pollinated flowers may be flagelliflorous (in which the inflorescence is projected beyond the crown profile of the tree on a long pedicel), as in *Oroxylum indicum* (Bignoniaceae) (Gould 1978), cauliflorous, as in *Syzygium cormiflorum* (Myrtaceae) (Crome and Irvine 1986) or more simply exerted from the foliage, as in *Passiflora mucronata* (Passifloraceae) (Sazima and Sazima 1978).

Within the group of plants described as bat-pollinated, floral morphology and phenology many serve to further restrict the utility of the resource to particular bats. In *Pseudobombax tomentosum* (Bombacaceae) in Brazil, the erect position and morphology of the flowers facilitate visits by large phyllostomid bats that land to feed but restrict visits by hover-feeding, small glossophagine bats (Gribel 1988).

Although many nectivorous birds and bats visit the same flowers their diurnal and nocturnal feeding patterns respectively mitigate against direct temporal foraging competition (Sussman and Raven 1978). The furred surface of floricolous bats has great pollen-carrying potential and bat pollination is recorded in many plant families (Marshall 1983; McCoy 1990; Kress and Stone 1993; Proctor and Yeo 1975; Faegri and van der Pijl 1979 and their references; Sazima and Sazima 1977, 1978; Armstrong 1979; Gould 1978; Scogin 1980; Kress 1985; Crome and Irvine 1986; Bawa 1990; Elmqvist, Cox, Rainey and Pierson 1992; Law 1992; Parry-Jones and Augee 1991a, 1991b). However, large megachiropteran fruit-bats, or flying foxes, are partly dystropic as the bats are sometimes destructive to blossoms (Faegri and van der Pijl 1979; Sussman and Raven 1978; Elmqvist, Cox, Rainey and Pierson 1992), yet they are able to transfer pollen at some reproductive cost to the plant. The pollen of chiropterophilous blossoms contains higher levels of protein than that of entomophilous blossoms (Raven, Evert and Curtis 1982). However, pollen is a complex structure and vertebrates demonstrate differential physiological abilities to utilize pollen as a nitrogen source (reviewed in Law 1992a, 1992b). Law (1992a) investigated physiological factors that influence pollen use by the Queensland blossom bat (*Syconycteris australis*), a specialized nectar and pollen feeder. Law (1992a) found that pollen digestion rates and alimentary retention time in addition to pollen type and size were primary determinants of the capacity of *S. australis* to efficiently use pollen. Thus physiological constraints, in combination with pollen size and structure (in addition to floral morphology, anthesis and nectar production and composition), are probably strong selective determinants of bat visitation to, and thus pollination of, rainforest plants.

Small blossom bats are significant nocturnal and crepuscular pollinators in tropical forests generally (Marshall 1983; Kress 1985; Sazima and Sazima 1977, 1978; Gould 1978: Crome and Irvine 1986; Sussman and Raven 1978) but the low nectar levels of blossoms of Australian rainforest trees at higher latitudes may be unable to fulfil the energy requirements of larger pteropodid bats (*Pteropus* spp.) (Scogin 1980; Williams 1993). Though considered partially dystropic by Faegri and van der Pijl (1979) and Elmqvist, Cox, Rainey and Pierson (1992), Pteropodidae contribute to the pollination of eucalypts (McCoy 1990; Eby 1991) and so the role of flying foxes in the pollination of mass-flowering rainforest Myrtaceae, and possibly Capparaceae, cannot be discounted. In addition, Floyd (1990) suggests cauliflorous *Hicksbeachia pinnatifolia* (Proteaceae), a tree restricted to the rainforests of northern New South Wales and south-east Queensland, to be bat pollinated. Williams (1993) however, found no evidence to support visitation or pollination of mass-flowering *Waterhousea floribunda* (Myrtaceae), by *Pteropus* spp., in a northern New South Wales lowland rainforest.

The single blossom bat occurring in New South Wales rainforests, *Syconycteris australis*, primarily visits trees with chiropterophilous blossoms but such flowers are absent or infrequent in Australian subtropical rainforests. *Banksia integrifolia* (Proteaceae) possesses an inflorescence that agrees in part with the chiropterophilous syndrome but the presence of *Banksia integrifolia* var. *integrifolia* in subtropical rainforests is restricted to coastal, littoral rainforests. *Banksia integrifolia* var. *compar*, however, can form a large tree in high altitude rainforests at similar latitudes (Boland, Brooker, Chippendale, Hall, Hyland, Johnston, Kleinig and Turner 1984). Taylor and Hopper (1988) do not list any bat species as pollinators of *Banksia integrifolia* although Law (1992a) studied *Syconycteris australis* visiting flowering *B. integrifolia* on the north coast of New South Wales. Parry-Jones and Augee (1991a, 1991b, 1992) recorded food items occurring in the droppings of *Pteropus poliocephalus* from the central coast of New South Wales. Parry-Jones and Augee (1991a, 1991b) identified pollen types found in samples as belonging to *Banksia serrata, B. integrifolia, Grevillea* sp. (*G. ?robusta*), *?Stenocarpus sinuatus* (Proteaceae), *Erythrina* sp. (Fabaceae), Lauraceae and Myrtaceae. These included native, introduced and cultivated plants. The proportion of myrtaceous pollen in samples ranged from 28 per cent to 86 per cent (Parry-Jones and Augee 1991a).

Pollination by Non-flying Mammals

Bawa (1990) considered the evidence supporting the transfer of pollen by non-flying mammals in tropical forests to be largely indirect and weak, and that flower visitation by such animals may be opportunistic and dystropic, being a response to the copious availability of food resources. However, as Bawa (1990) points out, the availability of floral food rewards to non-flying mammals may serve to provide resources during periods of low availability of fruit. Thus, the reproductive benefits may be measured as seed dispersal of genetic material.

There is, however, some recent evidence for pollination by mammals other than bats (e.g., Murawski, Hamrick, Hubbell and Foster 1990; Bertin 1989; Prance 1980; Gribel 1988; Lumer and Schoer 1986; Janson, Terborgh and Emmons 1981; Wiens and Rourke 1978; Sussman and Raven 1978). Sussman and Raven (1978) note that the regions in which pollination by non-flying mammals is more commonly recorded are those that have a depauperate flower visiting bat fauna (e.g., Madagascar, temperate Australia). Sussman and Raven (1978) suggested that non-flying mammal pollination systems may be relictual, resulting from more recent competitive displacement by flower visiting bats but these views were formed prior to many recent studies and may no longer have any basis. Examples of non-flying mammal pollinators include nocturnally-active lemurs (Lemuridae, Daubentoniidae) in Madagascar, bush-babies (*Galago* spp.) (Lorisidae) from West Africa and the "honey possum" *Tarsipes rostratus* (as *T. spencerae*) (Tarsipedidae) from south-west Australia (Sussman and Raven 1978).

General characteristics of the non-flying mammal pollination syndrome include dull coloured flowers in tight inflorescences strongly attached to stems, nocturnal anthesis and nectar production; copious nectar production; channelling of nectar to the ground; inflorescences positioned close to the ground (geoflorous) and hidden in foliage and a strong "musky" or "yeasty" odour (after Turner 1982; Wiens and Rourke 1978). These characteristics reflect nocturnal behaviour, poor colour reception, but well developed olfactory responses in many mammals.

Armstrong (1979), Turner (1982) and Carthew (1993) cite instances of flower visition and pollination by non-flying mammals in the Australian flora, but these are primarily non-rainforest examples, although some animals that include rainforest in their distribution were included (i.e., *Antechinus stuartii* — Dasyuridae; *Cercartetus nanus* — Burramyidae; *Trichosurus caninus, T. vulpecula* — Phalangeridae; *Rattus fuscipes* — Muridae). Rats are potential pollinators within the putative pollinator guild of *Balanophora fungosa* (Balanophoraceae), an herbaceous root parasite of Queensland rainforest trees (Irvine and Armstrong 1990). Pollination by small rodents is also recorded for Central American Melastomataceae (Lumer and Schoer 1986) and South African geoflorous *Protea* spp. (Weins and Rourke 1978), the latter additionally possessing cryptic blossoms obscured from external view by overhanging foliage. Proctor and Yeo (1975) (citing van der Pijl 1956) note apparent pollination, by introduced rats, of the Hawaiian, bird adapted, *Freycinetia arborea.*

In Australian rainforests there is a relatively large specialist arboreal mammal assemblage in tropical northeast Queensland (although the role, if any, of these species in pollination is unknown). In Australian subtropical and temperate rainforests the number of arboreal mammals is small, and none is a rainforest specialist (Winter 1988). It is unlikely that non-flying mammals are significant pollinators in southern rainforests.

DISCUSSION

The recent geological history of Australian rainforest, the spatial and temporal distribution of resources utilizable by pollinators, and the nature of floral structures in many tree species would all suggest that generalist rather than specialist pollination mechanisms would prevail in subtropical rainforest trees. The limited data available would support this conclusion but testing whether closely co-adapted, or specialist, plant — pollinator relationships are less common than generalist relationships will be important not only in a management context but may also affect how we look at rainforests more generally. Much of the public interest in rainforests arises from their species richness, and there is widespread recognition that, at the global scale, rainforests are the major centres of terrestrial biodiversity. This raises questions of why are rainforests so species rich and how is the richness related to ecosystem functioning? In relation to the latter question there is a popular perception of rainforests being organized like Swiss watches — a multitude of parts all essential for correct operation. If pollination is largely achieved by generalist pollinator guilds (composed of numerous and taxonomically diverse vectors each capable of undertaking pollination) then, at least for one very important component of rainforest function, the system would not resemble a Swiss watch suggesting that if there is a general explanation of rainforest species richness it does not uniquely reside in the complexity and organization of ecosystem processes.

Flexibility in pollination may have been a factor in the resilience of rainforest in the face of the rapid and massive environmental changes during the Quaternary. It may also enable species to survive and recover even when reduced to very small populations as a result of human activity, though some species may be at risk where fecundity (and hence ultimate population viability) is strongly density dependent and where populations have been reduced due to habitat fragmentation (see House 1993). Some of the rarest rainforest trees in northeastern New South Wales have populations of only a handful of individuals (Floyd 1990). Populations of this size might be too small to sustain a viable population of a specialist pollinator, but if the trees are capable of being pollinated by a range of vectors (even though some or all of these may be relatively inefficient) their chances of long-term survival may not be totally bleak. If species are also self-compatible then chances of survival will be further enhanced.

If, as Walker (1990) suggests, Australian rainforest tree species have not yet occupied their maximum ranges under the existing environmental conditions, then additional broadly composed pollinator complexes might be established as individual trees advance beyond the physiological or ecological limitations of existing pollinator guild components. The geographical ranges of rainforest trees and their pollinators are often dissimilar (Bawa 1990, quoting G. Stiles), which, in itself, implies an absence of tight fit and flexibility in the pollination system. Thus, the establishment of new pollinator complexes might reasonably be achieved by recruiting alternative pre-disposed pollinators from rainforest, and adjoining non-rainforest vegetation, as rainforest tree species expand their range, in addition to re-allocation or loss from within the existing pollinator guild.

Nevertheless we would argue that it is still necessary to manage sites so as to maximize the diversity of the pollinator guild. Not only is the conservation of biodiversity important in its own right but the diversity of the guild may confer resilience in the face of environmental change. If the diversity of the guild is severely reduced then there may be a risk that some functional subset essential for pollination of particular plants may be lost.

However, there are some plants with very specific pollination systems, these include *Eupomatia* and *Ficus*, in which the requirement extends to particular species of pollinator. In the case of those species which we postulate are pollinated by thrips the requirement may not be for individual thrips species but because of the specialized nature of the flower structure only thrips would be capable of effecting cross pollination. The specialized pollination in *Eupomatia* is of considerable interest given that *E. laurina* is regarded as one of the more primitive living angiosperms. Australian rainforests provide a refuge for a number of other primitive understorey shrubs and small trees; it would be of interest to know whether these species also have specialist pollination syndromes.

The majority of canopy and understorey trees in subtropical rainforest have relatively unspecialized flowers appropriate for generalist pollinators. There are obvious exceptions, some taxonomic, for example Proteaceae, which have more complex flowers, but there are few data on the pollinators of these species.

Amongst epiphytes and understorey herbs there are many examples of complex (for example in the orchids) or brightly coloured flowers (e.g., *Kreysigia multiflora* — Liliaceae) which may indicate specific pollinator requirements. While a generalist pollinator guild may be sufficient to sustain the canopy, managers should be aware of the possibility that the conservation of the total flora may require that attention be given to the needs of particular pollinating agents.

For species with no particular requirements, concurrently flowering plants may potentially compete with one another for a share of the pollinator pool, although from the point of view of the pollinators the availability of a range of "hosts" may serve to sustain and stabilize their populations (Waser and Read 1979; Heinrich and Raven 1972). More work on the phenology of tree species is required to determine whether competition occurs or whether there is sufficient separation of resource availability to provide a continuous sequence for the pollinator with minimum opportunities for competition.

Many questions as to the nature and function of pollinators in Australian rainforests remain unanswered. A by no means comprehensive list would include:

- how constant is the composition of the pollinator assemblage — does it vary in time and space?
- are there differences in the pollinator assemblages in different rainforest types?
- how widespread are self-incompatibility mechanisms in rainforest trees (an important question for the regeneration of isolated trees)?
- what are the limits to reduction of diversity of pollinator assemblages?
- are there more specialized plant-pollinator relationships in epiphytes and ground layer species than in the canopy, and, if so, are these vulnerable to disturbance?
- in the *Eupomatia/Elleschodes* system, where flowering events in a particular site may be separated by several years, how are *Elleschodes* populations maintained in the absence of flowers?

There are also many questions which cannot readily be addressed by investigation or experimentation but which might stimulate speculation, for example:

- what explanations can be offered for the rarity of bird pollination in Australia rainforests in view of the importance of honeyeaters in other ecosystems?
- has the spatial and temporal variation in tree distribution always favoured a preponderance of generalist pollination systems or did the post Miocene fragmentation and decline of rainforest cause a loss of specialist relationships?

Pollination in rainforests is only one of many aspects of ecosystem ecology which will need to be investigated if we are to have a basis for long-term management and conservation. We hope that this review may serve not only to stimulate interest in pollination ecology but in the wider problems of maintaining viable rainforests as part of Australia's, and the world's, biological heritage.

ACKNOWLEDGEMENTS

This paper would not have been possible without the diverse contributions (listed alphabetically, by institution) of Sally Durham, Dr Helene Martin, Dr Louise

Mazzaroli, Dr Charles Morris, Dr K. Parry-Jones, Dr Aola Richards, Debbie Stevenson (University of New South Wales, Kensington), Clarry Chadwick, Dr Mike Gray, Dr David McAlpine, Max Moulds, Colleen Pyne (The Australian Museum, Sydney), Dr Charles Bellamy (Transvaal Museum), Prof. L. A. Mound (The Natural History Museum, London), Dr W. D. J. Kirk (University of Keele, Keele), Dr T. F. Houston (Western Australian Museum, Perth), Mr K. Walker (Museum of Victoria, Melbourne), Josephine Cardale, Dr John Lawrence, Dr Ian Naumann (CSIRO, Canberra), Mr John Slack (NSW Department of Agriculture, Alstonville), Dr Shelley Barker (University of Adelaide) and Thusnelda Williams. Dr Daniel J. Bickel (The Australian Museum) helpfully commented on an earlier manuscript draft and Judy Thompson and Geoff Avern (The Australian Museum) are thanked for assistance with electron microscopy. One of us (G.W.) thanks the Australian Museum and the Australian Entomological Society for grants in aid of research.

REFERENCES

Ackerman, J. D., 1983. Diversity and seasonality of male euglossine bees (Hymenoptera:Apidae) in central Panama. *Ecology* **64:** 274–83.

Adam, P., 1987. New South Wales Rainforests: the nomination for the World Heritage List. National Parks and Wildlife Service, NSW: Sydney.

Adam, P., 1992. Australian Rainforests. Oxford University Press: Oxford.

Adam, P., Fisher, A. and Anderson, J. M. E., 1987. Pollen collection by honey bees from *Sarcocornia quinqueflora*. *Wetlands (Aust.)* **7:** 25–28.

Adams, P. B. and Lawson, S. D., 1993. Pollination in Australian orchids: a critical assessment of the literature 1882–1992. *Aust. J. Bot.* **41:** 553–75.

Adams, P. B., Bartareau, T. and Walker, K. L., 1992. Pollination of Australian orchids by *Trigona (Tetragona)* Jurine bees (Hymenoptera: Apidae). *Aust. Entomol. Mag.* **19:** 97–101.

Allsopp, P. G., 1992. Volatile compounds as attractants for *Campsomeris tasmaniensis* (Saussure) (Hymenoptera: Scoliidae). *Aust. Entomol. Mag.* **19:** 107–10.

Allsopp, P. G. and Cherry, R. H., 1991. Attraction of *Apis mellifera* L. (Hymenoptera: Apidae) to volatile compounds. *J. Aust. Entomol. Soc.* **30:** 219–20.

Anderson, A. B., Overal, W. L. and Henderson, A., 1988. Pollination ecology of a forest-dominant palm (*Orbignya phalerata* Mart.) in northern Brazil. *Biotropica* **20:** 192–205.

Appanah, S., 1981. Pollination in Malaysian primary forests. *The Malaysian Forester* **44:** 37–42.

Appanah, S., 1982. Pollination of androdioecious *Xerospermum intermedium* Radlk. (Sapindaceae) in a rainforest. *Biol. J. Linn. Soc.* **18:** 11–34.

Appanah, S., 1990. Plant-pollinator interactions in Malaysian rainforest. Pp. 85–100 in *Reproductive Ecology of Tropical Forest Plants* ed by K. S. Bawa and M. Hadley. Parthenon: Carnforth.

Appanah, S. and Chan, H. T., 1981. Thrips: the pollinators of some dipterocarps. *The Malaysian Forester* **44:** 234–52.

Appanah, S., Willemstein, S. C. and Marshall, A. G., 1986. Pollen foraging by two *Trigona* colonies in a Malaysian rainforest. *Malayan Nat. J.* **39:** 177–91.

Armbruster, W. S. and Webster, G. L., 1979. Pollination of two species of *Dalechampia* (Euphorbiaceae) in Mexico by euglossine bees. *Biotropica* **11:** 278–83.

Armstrong, J. A., 1979. Biotic pollination mechanisms in the Australian flora — a review. *NZ J. Bot.* **17:** 467–508.

Armstrong, J. A., Powell, J. M. and Richards, A. J. (eds), 1982. *Pollination and Evolution*. Royal Botanic Gardens: Sydney.

Armstrong, J. E. and Irvine, A. K., 1989a. Flowering, sex ratios, pollen-ovule ratios, fruit set and reproductive effort of a dioecious tree, *Myristica insipida* (Myristicaceae), in two different rainforest communities. *Am. J. Bot.* **76:** 74–85.

Armstrong, J. E. and Irvine, A. K., 1989b. Floral biology of *Myristica insipida* (Myristicaceae), a distinctive beetle pollination syndrome. *Am. J. Bot.* **76:** 86–94.

Armstrong, J. E. and Irvine, A. K., 1990. Functions of staminodia in the beetle-pollinated flowers of *Eupomatia laurina*. *Biotropica* **22:** 429–31.

Ashton, P. S., 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biol. J. Linn. Soc.* **1:** 155–96.

Ashton, P. S., Givnish, T. J. and Appanah, S., 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *Am. Natur.* **132:** 44–46.

Ashton, P. S., Soepadmo, E. and Yap, S. K., 1977. Current research into the breeding systems of rainforest trees and its implication. Pp. 187–92 in *Transactions of the International MAB — IUFRO Workshop on Tropical Rainforest Ecosystems and Resources* ed by E. F. Bruenig. Hamburg-Reinbek, 12–17 May 1977. Special Report No: 1. Chair of World Forestry: Hamburg-Reinbek.

Augspurger, C. K., 1980. Mass-flowering of a tropical shrub *(Hybanthus prunifolius)*: influence on pollinator attraction and movement. *Evolution* **34:** 475–88.

Baker, H. G., 1961. The adaption of flowering plants to nocturnal and crepuscular pollinators. *Quart. Rev. Biol.* **36:** 64–73.

Barford, A., Henderson, A. and Balslev, H., 1987. A note on the pollination of *Phytelephas microcarpa* (Palmae). *Biotropica* **19:** 191–92.

Barker, S., 1979. New species and a catalogue of *Stigmodera (Castiarina)* (Coleoptera: Buprestidae). *Trans. Roy. Soc. SA* **103:** 1–23.

Barker, S., 1986. *Stigmodera (Castiarina)* (Coleoptera: Buprestidae): taxonomy, new species and a checklist. *Trans. Roy. Soc. SA* **110:** 1–36.

Barlow, B. A., 1981. The Australian flora: its origin and evolution. *Flora of Australia* **1:** 25–75.

Barrows, E. M., 1977. Floral maturation and insect visitors of *Pachyptera hymenaea* (Bignoniaceae). *Biotropica* **9:** 133–34.

Barth, F. G., 1991. *Insects and Flowers*. Princeton University Press: Princeton.

Basset, Y., 1991. The seasonality of arboreal arthropods foraging within an Australian rainforest tree. *Ecol. Entomol.* **16:** 265–78.

Bateman, A. J., 1951. The taxonomic discrimination of bees. *Heredity* **5:** 271–83.

Bawa, K. S., 1974. Breeding systems of tree species of a lowland tropical community. *Evolution* **28:** 85–92.

Bawa, K. S., 1982. Outcrossing and the incidence of dioecism in island floras. *Am. Natur.* **119:** 866–71.

Bawa, K. S., 1990. Plant-pollinator interactions in tropical rainforests. *Ann. Rev. Ecol. Syst.* **21:** 399–422.

Bawa, K. S., 1992. Mating systems, genetic differentiation and speciation in tropical rainforest plants. *Biotropica* **24:** 250–55.

Bawa, K. S. and Crisp, J. E., 1980. Wind-pollination in the understorey of a rainforest in Costa Rica. *J. Ecol.* **68:** 871–76.

Bawa, K. S. and Ng, F. S. P., 1990. Phenology — commentary. Pp. 17–20 in *Reproductive Ecology of Tropical Forest Plants* ed by K. S. Bawa and M. Hadley. Unesco: Parthenon/Carnforth.

Beardsell, D. V., O'Brien, S. P., Williams, E. G., Knox, R. B. and Calder, D. M., 1993. Reproductive ecology of Australian Myrtaceae. *Aust. J. Bot.* **41:** 511–26.

Bell, W. J., 1990. Searching behaviour patterns in insects. *Ann. Rev. Entomol.* **35:** 447–67.

Bellamy, C. L., 1986. The higher classification of Australian Buprestidae, with description of a new genus and species (Coleoptera). *Aust. J. Zool.* **34:** 583–600.

Bernhardt, P. and Thien, L. B., 1987. Self-isolation and insect pollination in the primitive angiosperms: new evaluations of older hypotheses. *Plant Syst. Evol.* **156:** 159–76.

Bertin, R. I., 1989. Pollination Biology. Pp. 23–83 in *Plant-Animal Interactions* ed by W. G. Abrahamson. McGraw-Hill: New York.

Boland, D. J., Brooker, M. I. H., Chippendale, G. M., Hall, N., Hyland, B. P. M., Johnston, R. D., Kleinig, D. A. and Turner, J. D., 1984. *Forest Trees in Australia.* Nelson/C.S.I.R.O.: Melbourne.

Bolten, A. B. and Feinsinger, P., 1978. Why do hummingbird flowers secrete dilute nectar? *Biotropica* **10:** 307–09.

Boucek, Z., 1988. *Australasian Chalcidoidea (Hymenoptera). A biosystematic revision of genera of fourteen families, with a reclassification of species.* C.A.B. International: Wallingford.

Briggs, B. G. and Johnson, L. A. S., 1979. Evolution in the Myrtaceae — evidence from inflorescence structure. *Proc. Linn. Soc. NSW* **102:** 157–256.

Briggs, D. and Walters, S. M., 1984. *Plant Variation and Evolution.* Cambridge University Press: Cambridge.

Britton, E. B., 1970. Coleoptera. Pp. 495–621 in *The Insects of Australia.* C.S.I.R.O.: Melbourne.

Bronstein, J. L., 1988. Predators of fig wasps. *Biotropica* **20:** 215–19.

Brown, G. R., 1987. Revision of the Australian genus *Acanthothynnus* Turner (Hymenoptera: Tiphiidae). *J. Aust. Entomol. Soc.* **26:** 181–88.

Brown, G. R., 1989a. Revision of the Australian genus *Doratithynnus* Turner (Hymenoptera: Tiphiidae). *J. Aust. Entomol. Soc.* **28:** 1–17.

Brown, G. R., 1989b. The Australian genus *Encopothynnus* Turner (Hymenoptera: Tiphiidae). *J. Aust. Entomol. Soc.* **28:** 255–66.

Buchmann, S. L. and Buchmann, M. D., 1981. Anthecology of *Nouriri myrtilloides* (Melastomataceae: Memecyleae), and oil flower in Panama. *Biotropica Suppl.* **13:** 7–24.

Bullock, S. H., 1994. Wind pollination of neotropical dioecious trees. *Biotropica* **26:** 172–79.

Bullock, S. H., Martinez del Rio, and Ayala, R., 1989. Bee visitation rates to trees of *Prockia crucis* differing in flower number. *Oecologia (Berl.)* **78:** 389–93.

Cardale, J. C., 1993. Hymenoptera: Apoidea. *Zoological Catalogue of Australia* ed by W. W. K. Houston and G. V. Maynard. Australian Government Publishing Service: Canberra.

Carpenter, F. L., 1976. Plant-pollinator interactions in Hawaii: pollination energetics of *Metrosideros collina* (Myrtaceae). *Ecology* **57:** 1125–144.

Carthew, S. M., 1993. An assessment of pollinator visitation to *Banksia spinulosa. Aust. J. Ecol.* **18:** 257–68.

Chadwick, C. E., 1993. The roles of *Tranes lyteroides* and *T. sparsus* Boh (Col., Curculionidae) in the pollination of *Macrozamia communis* (Zamiaceae). Pp. 77–88 in *Proceedings of CYCAD 90, the Second International Conference of Cycad Biology* ed by D. W. Stevenson and N. J. Norstog. Palm and Cycad Societies of Australia Ltd: Milton, Brisbane.

Cole, B. J., 1981. Overlap, regularityand flowering phenologies. *Am. Natur.* **117:** 993–97.

Common, I. F. B., 1970. Lepidoptera. Pp. 365–866 in *The Insects of Australia.* C.S.I.R.O.: Melbourne.

Common, I. F. B., 1990. *Moths of Australia.* Melbourne University Press: Carlton.

Compton, S. G., Ross, S. J. and Thornton, I. W. B., 1994. Pollinator limitation of fig tree reproduction on the island of Anak Krakatau (Indonesia). *Biotropica* **26:** 180–86.

Crome, F. H. J. and Irvine, A. K., 1986. "Two Bob Each Way": The pollination and breeding system of the Australian rainforest tree *Syzygium cormiflorum* (Myrtaceae). *Biotropica* **18:** 115–25.

Crowson, R. A., 1981. *Biology of the Coleoptera.* Academic Press: London.

Crowson, R. A., 1988. Meligethinae as possible pollinators. *Entomol. General.* **14:** 61–62.

Crowson, R. A., 1990. A new genus of *Boganiidae* (Coleoptera) from Australia, with observations on glandular openings, cycad associations and geographical distribution in the family. *J. Aust. Entomol. Soc.* **29:** 91–99.

Cruden, A. W., 1972. Pollinators in high-elevation ecosystems: relative effectiveness of birds and bees. *Science N.Y.* **176:** 1439–440.

Dafni, A., 1992. *Pollination ecology: a practical approach.* Oxford University Press: Oxford.

Dayanandan, S., Attygalla, D. N. C., Abeygunasekera, A. W. W. L., Gunatilleke, I. A. U. N. and Gunatill, C. V. S., 1990. Phenology and floral morphology in relation to pollination of some Sri Lankan dipterocarps. Pp. 103–33 in *Reproductive Ecology of Tropical Forest Plants.* Unesco: Parthenon, Carnforth.

Diels, L., 1916. Kaferblumen bei den Ranales und ihre Bedeutung fur die Phylogenie der Angiospermen. *Berichte der Deutschen Botanischen Gesellschaft* **34:** 758–74.

Dodkin, D. S., 1987. Synchronous flower abscission in plants pollinated by hermit hummingbirds and the evolution of one-day flowers. *Biotropica* **19:** 90–93.

Dylewska, M., 1993. Apoidea (except Apidae) on the northern slopes of the Hohe Tauern Mts. *Acta zoologica cracoviensis* **35:** 509–64.

Eby, P., 1991. "Finger-winged night workers": managing forests to conserve the role of Grey-headed Flying Foxes as pollinators and seed dispersers. Pp. 91–100 in *Conservation of Australia's forest fauna* ed by D. Lunney. Royal Zoological Society of NSW: Mosman.

Elmqvist, T, Cox, P. A., Rainey, W. E. and Pierson, E. D., 1992. Restricted pollination on Oceanic islands: pollination of *Ceiba pentandra* by flying foxes in Samoa. *Biotropica* **24:** 15–23.

Elton, C. S., 1973. The structure of invertebrate populations inside neotropical rainforest. *J. Anim. Ecol.* **42:** 55–104.

Endress, P. K., 1984. The flowering process in the Eupomatiaceae (Magnoliales). *Botanische Jahrbuecher fur Systematik Pflanzengeschichte und Pflanzengeographie* **109:** 153–226.

Endrody-Younga, S. and Crowson, R. A., 1986. Boganiidae, a new beetle family for the African fauna. *Ann. Trans. Mus.* **34:** 253–73.

Ettershank, G. and Ettershank, J. A., 1990. Insects associated with flowers of Tasmanian leatherwoods (*Eucryphia* spp.). *Proc. Tas. Nat. Rainfor. Conserv. Progr. Rept No* **1:** 65–71.

Exley, E. M., 1968a. Revision of the genus *Brachyhesma* Michener (Apoidea: Colletidae). *Aust. J. Zool.* **16:** 167–201.

Exley, E. M., 1968b. Revision of the genus *Euryglossula* Michener (Apoidea: Colletidae). *Aust. J. Zool.* **16:** 203–17.

Exley, E. M., 1968c. Revision of the genus *Euryglossella* Cockerell (Apoidea: Colletidae). *Aust. J. Zool.* **16:** 219–26.

Exley, E. M., 1968d. *Quasihesma* — a new genus of Australian bees (Apoidea: Colletidae). *Aust. J. Zool.* **16:** 227–35.

Exley, E. M., 1968e. Revision of the genus *Euryglossina* Cockerell (Apoidea: Colletidae). *Aust. J. Zool.* **16:** 915–1020.

Exley, E. M., 1975. Revision of the genus *Hyphesma* Michener (Apoidea: Colletidae). *Aust. J. Zool.* **23:** 277–91.

Exley, E. M., Schneider, M. A. and Daniels, G., 1993. Bees (Hymenoptera) from Heathlands, Cape York Peninsula, Queensland. Pp. 149–54 in *Cape York Peninsula Scientific Expedition, Wet Season 1992 Report. Vol.* 2. The Royal Geographical Society of Queensland.

Faegri, K. and van der Pijl, L., 1979. *The Principles of Pollination Ecology.* Pergamon: Oxford.

Faegri, K., Iversen, J., Kaland, P. E. and Krzywinski, K., 1992. *Textbook of Pollen Analysis.* John Wiley and Sons: Chichester.

Feinsinger, P., Swarm, L. A. and Wolfe, J. A., 1985. Nectar-feeding birds on Trinidad and Tobago: comparison of diverse and depauperate guilds. *Ecol. Monogr.* **55:** 1–28.

Fischer, D. C. and Kogan, M., 1986. Chemoreceptors of adult Mexican bean beetles: external morphology and role in food preference. *Experi. Appl. Entomol.* **40:** 3–12.

Floyd, A. G., 1989. *Rainforest Trees of mainland south-eastern Australia.* Inkata Press/Forestry Commission of New South Wales: Sydney.

Floyd, A. G., 1990. *Australian Rainforests in New South Wales,* 2 vols. Surrey Beatty & Sons: Chipping Norton.

Ford, H. A., Paton, D. C. and Forde, N., 1979. Birds as pollinators of Australian plants. *NZ J. Bot.* **17:** 509–19.

Forster, P. I., 1989. Pollination of *Marsdenia fraseri* (Asclepiadaceae) by *Metriorrhynchus lateralis* (Coleoptera: Lycidae). *Coleopterists Bull.* **43:** 311–12.

Forster, P. I., 1992a. Pollination of *Hoya australis* (Asclepiadaceae) by *Ocybadistes walkerisothis* (Lepidoptera: Hesperiidae). *Aust. Entomol. Mag.* **19:** 39–43.

Forster, P. I., 1992b. Insects associated with the flowers of *Marsdenia cymulosa* Benth. (Asclepiadaceae) and their possible role in pollination. *Aust. Entomol. Mag.* **19:** 45–47.

Forster, P. I., Machin, P. J., Mound, L. and Wilson, G. W., 1994. Insects associated with reproductive structures of cycads in Queensland and northeast New South Wales, Australia. *Biotropica* **26:** 217–22.

Frankie, G. W., Opler, P. A. and Bawa, K. S., 1976. Foraging behaviour of solitary bees: implications for outcrossing of a neotropical forest tree species. *J. Ecol.* **64:** 1049–057.

Frith, C. B. and Frith, D. W., 1985. Seasonality of insect abundance in an Australian upland tropical rainforest. *Aust. J. Ecol.* **10:** 237–48.

Fuchs, G. V., 1974. Die gewinnung von pollen und nektar bei kafern. *Natur und Museum* **104:** 45–54.

Gardner, J. A., 1989. Revision of the genera of the tribe Stigmoderini (Coleoptera: Buprestidae) with a discussion of phylogenetic relationships. *Invertebr. Taxono.* **3:** 291–361.

Gautier-Hion, A., 1990. Interactions among fruit and vertebrate fruit eaters in an African Tropical Rainforest. Pp. 219–30 in *Reproductive Ecology of Tropical Forest Plants* ed by K. S. Bawa and M. Hadley. Unesco: Parthenon, Carnforth.

Gentry, A. H., 1978. Anti-pollinators for mass-flowering plants? *Biotropica* **10:** 68–69.

Gottsberger, G., 1974. The structure and function of the primitive angiosperm flower — a discussion. *Acta Botanica Neerlandica* **23:** 461–71.

Gottsberger, G., 1977. Some aspects of beetle pollination in the evolution of flowering plants. *Plant Syst. Evol. Suppl.* **1:** 211–26.

Gould, E., 1978. Foraging behaviour of Malaysian nectar-feeding bats. *Biotropica* **10:** 184–93.

Grant, V., 1949. Pollination systems as isolating mechanisms in ecosystems. *Evolution* **3:** 82–97.

Gribel, R., 1988. Visits of *Caluromys lanatus* (Didelphidae) to flowers of *Pseudobombax tomentosum* (Bombacaceae): a probable case of pollination by marsupials in Central Brazil. *Biotropica* **20:** 344–47.

Grinfeld, E. K., 1975. Anthophily in beetles (Coleoptera) and criticism of the cantharophilous hypothesis. *Entomologichesk̃eo Obozrenie* **54:** 18–22.

Gross, C. L., 1993. The breeding system and pollinators of *Melastoma affine* (Melastomataceae): a pioneer shrub in tropical Australia. *Biotropica* **25:** 468–74.

Guerrant, E. O. and Fiedler, P. L., 1981. Flower defenses against nectar-pilferage by ants. *Biotropica Suppl.* **13:** 25–33.

Haber, W. A., 1984. Pollination by deceit in a mass-flowering tropical tree *Plumeria rubra* (Apocynaceae). *Biotropica* **16:** 269–75.

Haber, W. A. and Frankie, G. W., 1989. A tropical hawkmoth community: Costa Rican dry forest Sphingidae. *Biotropica* **16:** 155–72.

Hacobian, B. S., 1992. New distribution records of the green tree ant *Oecophylla smaragdina* (Fabricius) (Hymenoptera: Formicidae: Formicinae) and three associated lycaenid butterflies. *Aust. Entomol. Mag.* **19:** 111–13.

Hamilton, A. G., 1897. On the fertilization of *Eupomatia laurina*. *Proc. Linn. Soc. NSW* **22:** 48–56.

Harden, G. (ed), 1990. *Flora of New South Wales Vol. 1.* NSW Univ. Press, Royal Botanical Gardens and Domain Trust: Sydney.

Harden, G. (ed), 1991. *Flora of New South Wales Vol. 2.* NSW Univ. Press, Royal Botanical Gardens and Domain Trust: Sydney.

Harden, G. (ed), 1992. *Flora of New South Wales Vol. 3.* NSW Univ. Press, Royal Botanical Gardens and Domain Trust: Sydney.

Harriss, F. C. L. and Beattie, A. J., 1991. Viability of pollen carried by *Apis mellifera* L., *Trigona carbonaria* Smith and *Vespula germanica* (F.) (Hymenoptera: Apidae, Vespidae). *J. Aust. Entomol. Soc.* **30:** 45–47.

Hawkeswood, T. J., 1978. Observations of some Buprestidae (Coleoptera) from the Blue Mountains, New South Wales. *Aust. Zool.* **19:** 257–75.

Hawkeswood, T. J., 1981a. Insect pollination of *Angophora woodsiana* F.M. Bail. (Myrtaceae) at Burbank, south-east Queensland. *Vict. Natur.* **98:** 120–29.

Hawkeswood, T. J., 1981b. Notes on the pollination of *Nuytsia floribunda* (Labill.) R.Br. (Loranthaceae) and some literature reviewed. *WA Nat.* **15:** 17–21.

Hawkeswood, T. J., 1982. Notes on insect pollination of two species of *Eucalyptus* (Myrtaceae) from south-west Western Australia. *Vict. Nat.* **99:** 28–37.

Heard, T. A., 1993. Pollinator requirements and flowering patterns of *Macadamia integrifolia*. *Aust. J. Bot.* **41:** 491–97.

Heideman, P. D., 1989. Temporal and spatial variation in phenology of flowering and fruiting in a tropical rainforest. *J. Ecol.* **77:** 1059–079.

Heinrich, B., 1975. Energetics of pollination. *Ann. Rev. Ecol. Syst.* **6:** 139–70.

Heinrich, B. and Raven, P. H., 1972. Energetics and pollination ecology. *Science N.Y.* **176:** 597–602.

Heithaus, E. R., 1979. Community structure of neotropical flower visiting bees and wasps: diversity and phenology. *Ecology* **60:** 190–202.

Herrera, C. M., 1988. Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. *Biol. J. Linn. Soc.* **35:** 95–125.

Hickman, J. C., 1974. Pollination by ants: a low energy system. *Science N.Y.* **184:** 1290–292.

Hiller, A., 1990. Notes on the systematics and biology of *Trichaulax* Kraatz (Coleoptera: Scarabaeidae: Cetoniinae). *Aust. Entomol. Mag.* **17:** 117–30.

Holldobler, B. and Wilson E. O., 1990. *The Ants.* Belknap Press: Cambridge.

Holloway, B. A., 1976. Pollen feeding in hover-flies (Diptera: Syrphidae). *NZ J. Zool.* **3:** 339–50.

Hopper, S. D., 1980. Pollination of the rainforest tree *Syzygium tierneyanum* (Myrtaceae) at Kuranda, Northern Queensland. *Aust. J. Bot.* **28:** 223–37.

Hotchkiss, A. T., 1958. Pollen and pollination in the Eupomatiaceae. *Proc. Linn. Soc. NSW* **83:** 86–91.

House, S. M., 1985. Relationships between breeding and spatial pattern in some dioecious tropical rainforest trees. Ph.D. Thesis. Australian National University: Canberra.

House, S. M., 1989. Pollen movement to flowering canopies of pistillate individuals of three rainforest tree species in tropical Australia. *Aust. J. Ecol.* **14:** 77–94.

House, S. M., 1992. Population density and fruit set in three dioecious tree species in Australian tropical rainforest. *J. Ecol.* **80:** 57–69.

House, S. M., 1993. Pollination success in a population of dioecious rainforest trees. *Oecologica (Berl.)* **96:** 555–61.

Houston, T. F., 1975. A revision of the Australian Hylaeine bees (Hymenoptera: Colletidae). 1. Introductory material and the genera *Heterapoides* Sandhouse, *Gephyrohylaeus* Michener, *Hyleoides* Smith, *Pharohylaeus* Michener, *Hemirhiza* Michener, *Amphylaeus* Michener and *Meroglossa* Smith. *Aust. J. Zool. Suppl. Ser. No.* **36.** 1–135.

Houston, T. F., 1984. Bionomics of a pollen-collecting wasp, *Paragia tricolor* (Hymenoptera: Vespidae: Masarinae), in Western Australia. *Rec. WA Mus.* **11:** 141–51.

Howe, H. F., 1990. Seed dispersal by birds and mammals: implications for seedling demography. Pp. 191–216 in *Reproductive Ecology of Tropical Forest Plants* ed by K. S. Bawa and M. Hadley. Unesco: Parthenon, Carnforth.

Howell, G. J., Slater, A. T. and Knox, R. B., 1993. Secondary pollen presentation in angiosperms and its biological significance. *Aust. J. Bot.* **41:** 417–38.

Hubbell, S. P., 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science N.Y.* **203:** 1299–309.

Inouye, D. W., 1993. *Pollination Biology Database.* University of Maryland: College Park.

Inouye, D. W. and Pyke, G. H., 1988. Pollination biology in the Snowy Mountains of Australia: comparisons with montane Colorada, USA. *Aust. J. Ecol.* **13:** 191–210.

Ippolito, A. and Armstrong, J. E., 1993. Floral biology of *Hornstedtia scottiana* (Zingiberaceae) in a lowland rainforest of Australia. *Biotropica* **25:** 281–89.

Irvine, A. K. and Armstrong, J. E., 1988. Beetle pollination in Australian tropical rainforests. *Proc. Ecol. Soc. Aust.* **15.**

Irvine, A. K. and Armstrong, J. E., 1990. Beetle pollination in tropical forests of Australia. Pp. 135–48 in *Reproductive Ecology of Tropical Forest Plants* ed by K. S. Bawa and M. Hadley. Unesco: Parthenon, Carnforth.

James, E. A. and Knox, R. B., 1993. Reproductive biology of the Australian species of the genus *Pandorea* (Bignoniaceae). *Aust. J. Bot.* **41:** 611–26.

Janson, C. H., Terborgh, J. and Emmons, L. H., 1981. Non-flying mammals as pollinating agents in the Amazonian forest. *Biotropica Suppl.* **13:** 1–6.

Janzen, D. H., 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science N.Y.* **171:** 203–05.

Janzen, D. H., 1977. Why don't ants visit flowers? *Biotropica* **9:** 252.

Janzen, D. H., 1979a. How to be a fig. *Ann. Rev. Ecol. Syst.* **10:** 13–51.

Janzen, D. H., 1979b. How many babies do figs pay for babies? *Biotropica* **11:** 48–50.

Jones, R. E. and Crome, F. H. J., 1990. The biological web–Plant/animal interactions in the rainforest. Pp. 74–87 in *Australian Tropical Rainforests* ed by L. J. Webb and J. Kikkawa. C.S.I.R.O: Australia.

Kato, M., Matsumoto, M. and Kato, T., 1993. Flowering phenology and anthophilous insect community in the cool-temperate subalpine forests and meadows at Mt. Kushigata in the central part of Japan. *Contributions from the Biological Laboratory Kyoto University* **28:** 119–72.

Kaul, R. B., Abbe, E. C. and Abbe, L. B., 1986. Reproductive phenology of the oak family (Fagaceae) in the lowland rainforests of Borneo. *Biotropica* **18:** 51–55.

Kearns, C. A. and Inouye, D. W., 1993. *Techniques for Pollination Biologists.* University Press of Colorado: Niwot.

Keller, S. and Armbruster, S., 1989. Pollination of *Hyptis capitata* by eumenid wasps in Panama. *Biotropica* **21:** 190–92.

Kevan, P. G., 1972. Collembola on flowers on Banks Island, N. W. T. *Quaestiones Entomologicae* **8:** 312–26.

Kevan, P. G., 1978. *Anthophilous springtails* (Collembola) from the Alaskan north slope, from Signy Island, Antarctica, and from near Ottawa, Ontario. *Rev. Ecol. Biol. Sci.* **15:** 373–78.

Kevan, P. G. and Baker, H. G., 1983. Insects as flower visitors and pollinators. *Ann. Rev. Entomol.* **28:** 407–53.

Kinnaird, M. F., 1992. Phenology of flowering and fruiting of an East African riverine forest system. *Biotropica* **24:** 187–94.

Kirk, W. D. J., 1985a. Effect of some floral scents on host finding by thrips (Insecta: Thysanoptera). *J. Chem. Ecol.* **11:** 35–43.

Kirk, W. D. J., 1985b. Pollen-feeding and host specificity and fecundity of flower thrips (Thysanoptera). *Ecol. Entomol.* **10:** 281–89.

Kirk, W. D. J., 1987. How much pollen can thrips destroy?. *Ecol. Entomol.* **12:** 31–40.

Kirk, W. D. J., 1988a. Assessing the effects of flower thrips. *Acta Phytopathologica et Entomologica Hungarica* **23:** 295–300.

Kirk, W. D. J., 1988b. Thrips and Pollination Biology. Pp. 129–35 in *Dynamics of Insect-Plant Interaction* ed by T. N. Ananthakrishnan and A. Raman. Oxford and IBH: New Delhi.

Kjellberg, F., Gouyon, P.-H., Ibrahim, M., Raymond, M. and Valdeyron, G., 1987. The stability of the symbiosis between dioecious figs and their pollinators: a study of *Ficus carica* L. and *Blastophaga psenes* L. *Evolution* **41:** 693–704.

Kress, W. J., 1985. Bat pollination of an Old World Heliconia. *Biotropica* **17:** 302–08.

Kress, W. J. and Stone, D. E., 1993. Morphology and floral biology of *Phenakospermum* (Strelitziaceae), an arborescent herb of the Neotropics. *Biotropica* **25:** 290–300.

Lack, A. J. and Kevan, P. G., 1984. On the reproductive biology of a canopy tree *Syzygium syzygioides* (Myrtaceae), in a rainforest in Sulawesi, Indonesia. *Biotropica* **16:** 31–36.

Law, B. S., 1992a. Physiological factors affecting pollen use by Queensland blossom bats *(Syconycteris australis). Funct. Ecol.* **6:** 257–64.

Law, B. S., 1992b. The maintenance nitrogen requirements of the Queensland blossom bat *(Syconycteris australis)* on a sugar/pollen diet: is nitrogen a limiting resource? *Physiol. Zool.* **65:** 634–48.

Lawrence, J. F. and Britton, E. B., 1991. Coleoptera. Pp. 543–683 in *The Insects of Australia.* Melbourne University Press: Melbourne.

Linhart, Y. B. and Mendenhall, J. A., 1977. Pollen dispersal by hawkmoths in a *Lindenia rivalis* Benth. population in Belize. *Biotropica* **9:** 143.

Lloyd, D. G. and Wells, M. S., 1992. Stigmatic exudate rewards and self-incompatibility in a primitive angiosperm, *Pseudowintera colorata* (Winteraceae). *Newsl. Aust. Poll. Ecol. Soc.* (July, unnumbered).

Lowman, M., 1982. Seasonal variation in insect abundance among three Australian rainforests with particular reference to phytophagous types. *Aust. J. Ecol.* **7:** 353–61.

Lumer, C. and Schoer, R. D., 1986. Pollination of *Blakea austin-smithii* and *B. penduliflora* (Melastomataceae) by small rodents in Costa Rica. *Biotropica* **18:** 363–64.

Marshall, A. G., 1983. Bats, flowers and fruit: evolutionary relationships in the Old World. *Biol. J. Linn. Soc.* **20:** 115–35.

Matthews, E. G. and Kitching, R. L., 1984. *Insect Ecology.* University Queensland Press: St. Lucia.

McAlpine, D. K., 1988. Studies in upside-down flies (Diptera: Neurochaetidae) Part II. Biology, adaptations, and specific mating mechanisms. *Proc. Linn. Soc. NSW* **110:** 59–82.

McCoy, M., 1990. Pollination of eucalypts by flying-foxes in Northern Australia. Pp. 33–37 in *Flying Fox Workshop Proceedings* ed by J. M. Slack. NSW Agriculture and Fisheries: Wollongbar.

McKeown, K. C., 1947. Catalogue of the Cerambycidae (Coleoptera) of Australia. *Mem. Aust. Mus.* **10:** 1–190.

Menzel, R. and Shmida, A., 1993. The ecology of flower colours and the natural colour vision of insect pollinators: the Isreali flora as a case study. *Biol. Rev.* **68:** 81–120.

Michener, C. D., 1970. Apoidea. Pp. 943–51 in *The Insects of Australia.* CSIRO: Melbourne.

Michener, C. D. and Houston, T. F., 1991. Apoidea. Pp. 993–1000 in *The Insects of Australia.* CSIRO: Melbourne.

Milton, K., 1991. Leaf change and fruit production in six neotropical Moraceae species. *J. Ecol.* **79:** 1–26.

Montalvo, A. M. and Ackerman, J. D., 1987. Limitations to fruit production in *Ionopsis utricularioides* (Orchidaceae). *Biotropica* **19:** 24–31.

Monteith, G. B., 1986. Some curious insect-plant associations in Queensland. *Qld Natur.* **26:** 105–14.

Mound, L., 1991. The first thrips species (Insecta, Thysanoptera) from cycad male cones, and its family level significance. *J. Nat. Hist.* **25:** 647–52.

Murawski, D. A. and Hamrick, J. L., 1992. The mating system of *Cavanillesia platanifolia* under extremes of flowering-tree density: a test of predictions. *Biotropica* **24:** 99–101.

Murawski, D. A., Hamrick, J. L., Hubbell, S. P. and Foster, R. B., 1990. Mating systems of two Bombacaceous trees of a neotropical moist forest. *Oecologia (Berl.)* **82:** 501–06.

Naumann, I. D., 1991. Hymenoptera. Pp. 911–1000 in *The Insects of Australia.* CSIRO: Melbourne.

Newstrom, L. E., Frankie, G. W. and Baker, H. G., 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain forest at La Selva, Costa Rica. *Biotropica* **26:** 141–59.

Nilsson, L. A. Jonsson, L., Ralison, L. and Randrianjohany, E., 1987. Angraecoid orchids and hawkmoths in Central Madagascar: specialized pollination systems and generalist foragers. *Biotropica* **19:** 310–18.

Norstog, K. J., Stevenson, D. W. and Niklas, K. J., 1986. The role of beetles in the pollination of *Zamia furfuracea* L.fil. (Zamiaceae). *Biotropica* **18:** 300–06.

Ornduff, R., 1989. Size distribution and coning behaviour of the Australian cycad *Lepidozamia peroffskyana*. *Aust. J. Ecol.* **14:** 241–45.

Ornduff, R., 1990. Geographic variation in reproductive behaviour and size structure of the Australian cycad *Macrozamia communis* (Zamiaceae). *Amer. J. Bot.* **77:** 92–99.

Papaj, D. R. and Prokopy, R. J., 1989. Ecological and evolutionary aspects of learning in phytophagous insects. *Ann. Rev. Entomol.* **34:** 315–50.

Parry-Jones, K. A. and Augee, M. L., 1991a. Food selection by Grey-headed flying foxes *(Pteropus poliocephalus)* occupying a summer colony site near Gosford, New South Wales. *Wildl. Res.* **18:** 111–24.

Parry-Jones, K. A. and Augee, M. L., 1991b. The diet of flying-foxes in the Sydney and Gosford areas of New South Wales, based on sighting reports 1986–1990. *Aust. Zool.* **27:** 49–54.

Parry-Jones, K. A. and Augee, M. L., 1992. Movements of Grey-headed flying foxes *(Pteropus poliocephalus)* to and from a colony site on the central coast of New South Wales. *Wildl. Res.* **19:** 331–40.

Paton, D. C., 1993. Honeybees in the Australian environment. *BioScience* **43:** 95–103.

Peakall, R., Beattie, A. J. and James, S. H., 1987. Pseudocopulation of an orchid by male ants : a test of two hypotheses accounting for the rarity of ant pollination. *Oecologia (Berl.)* **73:** 522–24.

Pemberton, C. E., 1934. Fig wasps established on Kauai. *Proc. Hawaiian Entomol. Soc.* **8:** 379.

Perry, D. R. and Starrett, A., 1980. The pollination ecology and blooming strategy of a neotropical emergent tree, *Dipteryx panamensis*. *Biotropica* **12:** 307–13.

Petanidou, T. and Ellis, W. N., 1993. Pollinating fauna of a phryganic ecosystem: composition and diversity. *Biodiver. Lett.* **1:** 9–22.

Pizzey, G., 1982. *A Field Guide to Birds of Australia.* Collins: Sydney.

Prance, G. T., 1980. A note on the probable pollination of *Combretum* by *Cebus* monkeys. *Biotropica* **12:** 239.

Primack, R. B., 1978. Variability in New Zealand montane and alpine pollinator assemblages. *NZ J. Ecol.* **1:** 66–73.

Primack, R. B., 1985. Longevity of individual flowers. *Ann. Rev. Ecol. Syst.* **16:** 15–37.

Primack, R. B. and Hall, P., 1992. Biodiversity and forest change in Malaysian Borneo. *BioScience* **42:** 829–37.

Proctor, M. and Yeo, P., 1975. *The Pollination of Flowers.* Collins: London.

Proenca, C. E. B. and Gibbs, P. E., 1994. Reproductive biology of eight sympatric Myrtaceae from Central Brazil. *New Phytol.* **126:** 343–54.

Pyke, G. H., 1991. What does it cost a plant to produce floral nectar? *Nature* **350:** 58–59.

Pyke, G. H. and Balzer, L., 1985. The effects of the introduced honeybee *(Apis mellifera)* on Australian native bees. A report prepared for NSW National Parks and Wildlife Service. Occasional Papers of the New South Wales National Parks and Wildlife Service: Sydney.

Ramsay, M. W., 1988. Differences in pollinator effectiveness of birds and insects visiting *Banksia menziesii* (Proteaceae). *Oecologia (Berl.)* **76:** 119–24.

Rathcke, B. and Lacey, E. P., 1985. Phenological patterns of terrestrial plants. *Ann. Rev. Ecol. Syst.* **16:** 179–214.

Rausher, M. D. and Fowler, N. L., 1979. Intersexual aggression and nectar defense in *Chauliognathus distinguendus* (Coleoptera: Cantharidae). *Biotropica* **11:** 96–100.

Raven, P. H., Evert, R. F. and Curtis, H., 1982. *Biology of Plants.* Worth: New York.

Read, J., 1989. Phenology and germination in some rainforest canopy species at Mt. Field National Park, Tasmania. *Pap. Proc. Roy. Soc. Tas.* **123:** 211–21.

Real, L. A., 1981. Nectar availability and bee foraging on *Ipomoea* (Convolulaceae). *Biotropica Suppl.* **13:** 64–69.

Richards, A. O. and Filewood, L. W., 1990. Feeding behaviour and food preferences of the pest species comprising the *Epilachna vigintiopunctata* (F.) complex (Col., Coccinellidae). *J. Appl. Entomol.* **110:** 501–15.

Riek, E. F., 1970. Hymenoptera. Pp. 867–959 in *The Insects of Australia.* CSIRO: Melbourne.

Robinson, L., 1991. *A Field Guide to the Native Plants of the Sydney Region.* Kangaroo Press: Kenthurst.

Roubik, D. W., 1982. Obligate necrophagy in a social bee. *Science N.Y.* **217:** 1059–060.

Roubik, D. W., 1989. *Ecology and natural history of tropical bees.* Cambridge University Press: Cambridge.

Roubik, D. W. and Ackerman, J. D., 1987. Long-term ecology of euglossine orchid-bees (Apidae:Euglossini) in Panama. *Oecologia (Berl.)* **73:** 321–33.

Russell-Smith, J. and Lee, A. H., 1992. Plant populations and monsoon rain forest in the Northern Territory, Australia. *Biotropica* **24:** 471–87.

Sands, D. and House, S., 1990. Plant/Insect interactions — Food webs and breeding systems. Pp. 88–97 in *Australian Tropical Rainforests* ed by L. J. Webb and J. Kikkawa. CSIRO: Melbourne.

Saunders, D. S., 1977. *An Introduction to Biological Rhythms.* Blackie and Sons: London.

Sazima, I. and Sazima, M., 1977. Solitary and group foraging: two flower-visiting patterns of the lesser spear-nosed bat *Phyllostomus discolor*. *Biotropica* **9:** 213–15.

Sazima, M. and Sazima, I., 1978. Bat pollination of the passion flower, *Passiflora mucronata* in Southeastern Brazil. *Biotropica* **10:** 100–09.

Scambler, D. J., 1993. Ischnauchen, a new genus for *Aphiorhynchus costatus* McKeown (Coleoptera: Cerambycidae). *J. Aust. Entomol. Soc.* **32:** 193–95.

Schatz, G. E., 1990. Some aspects of pollination biology in Central American forests. Pp. 69–81 in *Reproductive Ecology of Tropical Forest Plants* ed by K. S. Bawa and M. Hadley. Unesco: Parthenon, Carnforth.

Schemske, D. W., 1980. Floral ecology and hummingbird pollinations of *Combretum farinosum* in Costa Rica. *Biotropica* **12:** 169–81.

Schubart, H. O. R. and Anderson, A. B., 1978. Why don't ants visit flowers? A reply to D.H. Janzen. *Biotropica* **10:** 310–11.

Scogin, R., 1980. Floral pigments and nectar constituents of two bat-pollinated plants: coloration, nutritional and energetic considerations. *Biotropica* **12:** 273–76.

Seeley, T. D., 1983. The ecology of temperate and tropical honeybee societies. *Amer. Sci.* **71:** 264–72.

Seifert, R. P., 1982. Neotropical *Heliconia* insect communities. *Quart. Rev. Biol.* **57:** 1–28.

Selander, R. B., 1957. The systematic position of the genus *Nephrites* and the phylogenetic relationships of the higher groups of Rhipiphoridae (Coleoptera). *Ann. Entomol. Soc. Amer.* **50:** 88–103.

Sharma, N., Koul, P. and Koul, A. K., 1993. Pollination biology of some species of genus *Plantago* L. *Bot. J. Linn. Soc.* **111:** 129–38.

Snow, A. A. and Roubik, D. W., 1987. Pollen deposition and removal of bees visiting two tree species in Panama. *Biotropica* **19:** 57–63.

Steiner, K. E., 1985. The role of nectar and oil in the pollination of *Drymonia serrulata* (Gesneriaceae) by *Epicharis* bees (Anthophoridae) in Panama. *Biotropica* **17:** 217–29.

Stephenson, A. G., 1982. When does outcrossing occur in a mass-flowering plant? *Evolution* **36:** 762–67.

Stiles, G., 1977. Co-adapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science N.Y.* **198:** 1177–178.

Stratton, D. A., 1989. Longevity of individual flowers in a Costa Rican cloud forest: ecological correlates and phylogenetic constraints. *Biotropica* **21:** 308–18.

Sugden, E. A. and Pyke, G. H., 1991. Effects of honey bees on colonies of *Exoneura asimillima*, an Australian native bee. *Aust. J. Ecol.* **16:** 171–81.

Summerbell, G., 1991. Regeneration of complex notophyll vine forest (humid subtropical rainforest) in eastern Australia — a review. *Cunninghamia* **2:** 391–410.

Sussman, R. W. and Raven, P. H., 1978. Pollination by lemurs and marsupials: an archaic co-evolutionary system. *Science N.Y.* **200:** 731–36.

Taylor, A. and Hopper, S., 1988. *The Banksia Atlas.* Australian Flora and Fauna Series. Number 8. Australian Government Publishing Service: Canberra.

Terborgh, J., 1990. Seed and fruit dispersal — commentary. Pp. 181–90 in *Reproductive Ecology of Tropical Forest Plants* ed by K. S. Bawa and M. Hadley. Unesco: Parthenon, Carnforth.

Thien, L. B., 1980. Patterns of pollination in the primitive angiosperms. *Biotropica* **12:** 1–13.

Toledo, V. M., 1977. Pollination of some rainforest plants by non-hovering birds in Vera Cruz, Mexico. *Biotropica* **9:** 262–67.

Truswell, E. M., 1990. Australian Rainforests: the 100 million year record. Pp. 7–22 in *Australian Tropical Rainforests* ed by L. J. Webb and J. Kikkawa. CSIRO: Melbourne.

Turner, V., 1982. Marsupials as pollinators in Australia. Pp. 55–66 in *Pollination and Evolution* ed by J. A. Armstrong, J. M. Powell and A. J. Richards. Royal Botanic Gardens: Sydney.

Uhl, N. W. and Moore, H. E., 1977. Correlations in inflorescence, flower structure and floral anatomy with pollination in some palms. *Biotropica* **9:** 170–90.

Vithanage, V. and Ironside, D. A., 1986. The insect pollinators of Macadamia and their relative importance. *J. Aust. Instit. Agri. Sci.* **52:** 155–60.

Walker, D., 1990. Directions and rates of tropical rainforest processes. Pp. 23–32 in *Australian Tropical Rainforests* ed by L. J. Webb and J. Kikkawa. CSIRO: Melbourne.

Walker, K. L., 1986. Revision of the Australian species of the genus *Homalictus* Cockerell (Hymenoptera: Halictidae). *Mem. Mus. Vict.* **47:** 105–200.

Ware, A. B. and Compton, S. G., 1992. Breakdown of pollinator specificity in an African fig tree. *Biotropica* **24:** 544–49.

Waser, N. M. and Real, L. A., 1979. Effective mutualism between sequentially flowering plant species. *Nature* **281:** 670–72.

Webb, C. J., 1984. Flower and fruit movements in *Muntingia calabura*: a possible mechanism for avoidance of pollinator-disperser interference. *Biotropica* **16:** 37–42.

Webb, G. A., 1986a. Some insect pollinators of *Kunzea ambigua* (Sm.) Druce (Myrtaceae) near Sydney, New South Wales. *Vict. Natur.* **103:** 12–15.

Webb, G. A., 1986b. Flower-visiting beetles of some New South Wales *Leptospermoidea*. *Vict. Natur.* **103:** 170–74.

Webb, G. A., 1989. Insects as potential pollinators of *Micromyrtus ciliata* (Sm.) Druce, Myrtaceae. *Vict. Natur.* **106:** 148–51.

Wheelwright, N. T. and Orians, G. H., 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology and constraints on co-evolution. *Amer. Natur.* **119:** 402–13.

Wiebes, J. T., 1963, Indo-Malayan and Papuan fig wasps (Hymenoptera, Chalcidoidea). 2. The genus *Pleistodontes* Saunders (Agaonidae). *Zool. Meded. Leiden* **38:** 303–21.

Wiebes, J. T., 1979. Co-evolution of figs and their insect pollinators. *Ann. Rev. Ecol. Syst.* **10:** 1–12.

Wiens, D. and Rourke, J. P., 1978. Rodent pollination in southern African *Protea* spp. *Nature* **276:** 71–73.

Williams, E. C., Knox, R. B., Gilbert, J. H. and Bernhardt, P. (eds), 1982. *Pollination 82.* School Botany University of Melbourne: Melbourne.

Williams, G. A., 1993. *Hidden Rainforests: subtropical rainforest and their invertebrate biodiversity.* New South Wales University Press — The Australian Museum: Sydney.

Williams, G. A. and Adam, P., 1993. Ballistic pollen release in Australian members of the Moraceae. *Biotropica* **25:** 478–80.

Williams, G. A. and Adam, P., in press. Records of aculeate wasps from flowering subtropical rainforest trees. *Aust. Entomol.*

Williams, G. A. and Williams, T., 1983. A list of the Buprestidae (Coleoptera) of the Sydney Basin, New South Wales, with adult food plant records and biological notes on food plant associations. *Aust. Entomol. Mag.* **9:** 81–93.

Williams, J. B., Harden, G. J. and McDonald, W. J. F., 1984. *Trees and Shrubs in Rainforests of New South Wales and Southern Queensland.* University of New England: Armidale.

Williams, N. H. and Dodson, C. H., 1971. Selective attraction of male euglossine bees to orchid floral fragrances and its importance in long distance pollen flow. *Evolution* **26:** 84–95.

Willmer, P. G., 1988. The role of insect water balance in pollination ecology: *Xylocopa* and *Calotropis*. *Oecologia (Berl.)* **76:** 430–38.

Winter, J. W., 1988. Ecological specialization of mammals in Australian tropical and sub-tropical rainforest: refugial or ecological determinism? *Proc. Ecol. Soc. Aust.* **15:** 127–38.

Wolda, H., 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. *J. Anim. Ecol.* **47:** 369–81.

Young, J. H., 1990. Pollination and reproductive biology of an understorey neotropical aroid. Pp. 151–63 in *Reproductive Ecology of Tropical Forest Plants* ed by K. S. Bawa and M. Hadley. Unesco: Parthenon, Carnforth.

BOOK REVIEWS — BOOK REVIEWS

"The Mountain Pygmy-possum of the Australian Alps" by Ian Mansergh and Linda Broom. 1994.
Illustrations by Katrina Sandiford.
Australian Natural History Series, New South Wales University Press, Kensington.
114 pages. ISBN O 86840 085 8. RRP $19.95.

The story of this tiny possum has an unparalleled fascination for all mammalogists in Australia and Ian Mansergh and Linda Broome have captured some of the magic in this book. Much of our knowledge of the species has come through their dedicated research within the last 10 years and it is excellent to see that information brought together in a compact form within the Australian Natural History Series.

The book presents the story of the discovery and life history of *Burramys* and the challenge of its conservation in the ski-fields of the Australian Alps. It also draws out the contrasts and similarities between Burramys and other pygmy-possums. Mostly it is simply written and the facts are clearly presented. Not surprisingly, the weakest parts of the text are where the knowlege is incomplete, but they nicely argue the value of continued research to uncover this information.

Unfortunately, some of the black-and-white photographs are too dark to show the features being described and histograms and other graphics with four shadings are difficult to read. Apart from these production faults, there is little to criticize and much to praise. I would recommend it to any person with an interest in life history studies or ecology, for it presents a well balanced, logical sequence of research leading to answers to specific ecological questions. Because this research has been so focused on conservation and management, it stands as a model for us all.

Dr Judy Caughley
Bureau of Resource Sciences
Canberra